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CONTENTS

Anatomy and Reproductive Biology of Two Western Atlantic Species of Vitrinellidae, With a Case of Protandrous Hermaphroditism in the Rissoacea

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ABSTRACT

Two western Atlantic vitrinellids, *Cyclostremiscus beauii* (Fischer, 1857) and *Circulus texanus* (Moore, 1965) new combination are redescribed based on a study of live snails from the burrows of the stomatopod crustacean *Lysiosquilla scabricauda* (Lamarck, 1818). Anatomy and reproductive biology are emphasized, with the first recorded description of spawn and larval development in the family. Synonymies are given, and a lectotype is selected for *Cy. beauii*. Literature data concerning anatomy are reviewed for the marine near-planispiral rissoaceans; Vitrinellidae (including *Cyclostremiscus* and *Circulus*, with Circulidae as a synonym) is considered distinct from Tornidae. Unusual morphological aspects of *Cy. beauii* are discussed, including external ciliation patterns, pallial tentacles (which are functionally and morphologically different from each other), and stomach morphology (with a large posterior chamber). Protandrous sequential hermaphroditism in *Cy. beauii* is inferred (for the first time in the Rissoacea) from morphological evidence of sex change correlated with size.

Key words: *Cyclostremiscus*; *Circulus*; Vitrinellidae; Tornidae; Rissoacea; systematics; anatomy; hermaphroditism.

INTRODUCTION

Despite the great number of nominal species assigned to the poorly defined, cosmopolitan, marine rissoacean family Vitrinellidae Bush, 1897, little is known about the biology of its members. Their small size, mostly unknown habitats, poor representation in collections, and frequent confusion with other small-shelled members of groups such as Cyclostrematidae Fischer, 1885, Skeneidae Thiele, 1929, Turbinidae Rafinesque, 1815, and Tornidae Sacco, 1896, may account for the lack of attention paid to this family, and why authors who have attempted revisions (*e.g.*, Tryon, 1888; Bush, 1897; Melvill, 1906; Pilsbry & Olsson, 1945; Pilsbry & McGinty, 1945a,b, 1946a,b, 1950; Laseron, 1958; Moore, 1964; Adam & Knudsen, 1969) relied almost entirely on shell characters to distinguish taxa on all taxonomic levels.

Aside from Pilsbry and McGinty's (1945a, 1946b) sketches of crawling animals of several nominal genera,

and studies on the gross morphology of *Cochliolepis parasitica* Stimpson, 1858 (by Moore, 1972) and *C. albicerata* Ponder, 1966 (by Ponder, 1966), published information on anatomy is available for only one species of this family, *Circulus striatus* (Philippi, 1836) from the eastern Atlantic. Data on *Ci. striatus*, extensively presented by Fretter (1956) and later summarized by Fretter and Graham (1962, 1978), were based on material which Fretter and Graham (1978:228) described as "the only live specimens . . . obtained by Fretter (1956) from the stomach of the starfish *Astropecten* . . . dredged on sandy bottoms 28–30 m deep in the Gulf of Gascony."

Thus, the present concept of vitrinellid anatomy is based mainly on Fretter's description of a single species, *Circulus striatus*, the type species of the name-bearing genus of the nominal family Circulidae (see Discussion, below). Discussions of phylogenetic relationships (or synonymies) between families such as Vitrinellidae and Tornidae have demonstrated the need for anatomical and reproductive data for these groups (*e.g.*, Fretter, 1956; Taylor & Sohl, 1962; Moore, 1965; Golikov & Starobogatov, 1975; Boss, 1982; Graham, 1982; Ponder, in press).

Studies on two species of western Atlantic Vitrinellidae are reported herein. Populations of *Cyclostremiscus beauii* (Fischer, 1857) and *Circulus texanus* (Moore, 1965) were discovered in Florida in sand-flat burrows of the stomatopod crustacean *Lysiosquilla scabricauda* (Lamarck, 1818). These burrows are U-shaped and extend up to 1.5 m into the sediment, with horizontal distances of 6–7 m between the two openings; a pair of stomatopods inhabits each burrow system, maintaining it over long periods of time (Serène, 1954; R. B. Manning, personal communication). *Cyclostremiscus beauii*, with a shell diameter of 6–8 mm, is one of the largest vitrinellids, a fact that facilitated detailed study of its morphology and anatomy and allowed a test of Fretter's hypothesis that some of the characters found in the much smaller (2 mm) *Circulus striatus* are size-related (Fretter, 1956:380).

Special emphasis was placed upon characters of the reproductive system, for which Moore (1964:18) noted "Nothing is known of the reproduction of the family

except that the animals are dioecious, and that the male is provided with a penis." Data presented herein suggest that *Cy. beauii* is a protandrous sequential hermaphrodite. Only incomplete data are available for *Circulus texanus*, as animals of this species were collected only twice, both times before the actual beginning of this study. However, since gross anatomy, spawn, and developing eggs were observed for this species, available data are presented here.

MATERIAL AND METHODS

Samples were taken from stomatopod burrows in shallow-water sand flats in the Indian River lagoon just inside the Ft. Pierce Inlet, St. Lucie County, eastern Florida (27°28.3'N, 80°17.9'W) using a stainless steel bait pump ("yabby pump") in conjunction with sieves of 1–2 mm mesh. Depths at low tide ranged from less than 0.5 m to supratidal, wherein the water level lay several centimeters below the level of the sand.

Living snails were maintained in finger bowls of seawater at room temperature (24 °C). Carmine and fluorescein sodium particles were used to observe ciliary action and currents produced by the animals. For gross dissections, shells were cracked and animals subsequently relaxed using magnesium sulfate crystals ("epsom salts"). Other anaesthetic chemicals (7% magnesium chloride in distilled water, menthol crystals) were tried but produced little or no effect with gradual addition, or too strong an effect resulting in retraction. Methylene-blue/basic-fuchsin and neutral red were used to better delineate tissues and organs in gross dissections. Structures and organs were measured following in part the outline given by Davis and Carney (1973: fig. 4A). Terminology of the nervous system is after Davis *et al.* (1976).

For histological sectioning, animals were relaxed as above and fixed in either glutaraldehyde-formalin solution (4% formalin, 2.5% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2) or 5% buffered formalin (Humason, 1962:14). Shells were either broken and removed, or dissolved in a 1% solution of ethylene diamine tetraacetic acid (EDTA, adjusted to pH 7.2). Specimens were embedded in paraffin, sectioned at 5–7 μm and stained with Alcian Blue/Periodic-Acid-Schiff (PAS), counterstained with Harris' Hematoxylin/Eosin (Humason, 1962: 125, 269, 298). Staining reactions described in the text refer to this method unless otherwise noted. Photomicrographs of sections were taken with a Zeiss Photomicroscope-3.

Radulae and jaws were extracted by dissolving the surrounding soft tissue in a solution of 10% sodium hydroxide. Spermatozoa were prepared for SEM by placing a drop of concentrated sperm in seawater onto a coverslip placed in a covered petri dish containing droplets of 25% glutaraldehyde, and passing the coverslip through an ethanol series ending in acetone, and then critical-point drying the sample. Whole animals were fixed, passed through an ethanol series, transferred to amyl acetate, and critical-point dried. These, together with air-dried

shells, radulae, jaws, and opercula were coated with gold/palladium, and scanned using a Zeiss Novascan-30. Figures 1–3 were photographed using a Hitachi S-570 scanning electron microscope. Radular terminology is after Bandel (1984:3).

Protoconch and teleoconch diameters were recorded as the greatest dimension perpendicular to the columellar axis. Teleoconch height was the greatest dimension parallel to the columellar axis, measured from the apex to the base of the aperture. Umbilical diameter was the greatest distance between the columellar lip and the most prominent portion of the umbilical wall, measured in ventral view. Teleoconch whorls were counted from the protoconch II–teleoconch line to the farthest extent of the periphery (= the point on the outer lip used for greatest shell diameter). The number of protoconch whorls was determined by the method of Taylor (1975:10; summarized by Jablonski & Lutz, 1980:332, fig. 4).

Cited repositories are (* indicates location of voucher material):

ANSP—Academy of Natural Sciences of Philadelphia, PA.
CAS—California Academy of Sciences, San Francisco.
*IRCZM—Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution (HBOI), Ft. Pierce, FL.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, MA.
MNHN—Muséum National d'Histoire Naturelle, Paris.
*RSMAS—Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, FL.
UNC-IMS—Institute of Marine Sciences, University of North Carolina, Morehead City, NC.
*USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC.

RESULTS

Rissoacea Gray, 1847

= Truncatellacea Gray, 1840, "submission to be made to ICZN to suppress this name" (Ponder, 1985:15).

Vitrinellidae Bush, 1897

Cyclostremiscus Pilsbry & Olsson, 1945:266.

Type species: *Vitrinella panamensis* C. B. Adams, 1852 (by original designation).

Cyclostremiscus beauii (Fischer, 1857) (figures 1–52; tables 1, 2)

Adeorbis Beauii Fischer, 1857a:173 [*nomen nudum*].
Adeorbis Beauii Fischer, 1857b:286, pl. 10, fig. 12 [Guadeloupe].—Bush, 1897:104.
Cyclostrema Beani [sic].—A. Adams, 1866:251, pl. 255, fig. 25 [after Fischer, 1857b].
Cyclostrema bicarinata Guppy, 1866:291, pl. 17, figs. 5a,b ["Miocene" (Lower Pliocene), Jamaica].

Skenea sulcata "Bush" Simpson, 1887:61 [*nomen nudum*; see Moore, 1964 131].

Adeorbis Beaui.—Dall, 1889:150; 1892:345.

Adeorbis Beaui var. *bicarinata*.—Dall, 1903:1595 ["Oligocene," Jamaica].

"*Circulus*" *bicarinatus*.—Woodring, 1928:439, pl. 37, figs. 10–12 [neotype designation].

"*Adeorbis*" *beaui*.—Woodring, 1928:440.

Circulus stirophorus M. Smith, 1937:67, pl. 6, figs. 2a,b [Pliocene, Florida].

Cyclostrema angulata.—Hertlein & Strong, 1951:110 [West Indies].

Cyclostremiscus (Ponocyclus) beaui bicarinatus.—Pilsbry, 1953: 427, pl. 55, figs. 1–1e.

Vitrinella (Solariorbis) beaui.—Abbott, 1954.138.

Vitrinella beaui.—Wells *et al.*, 1961:267.

Cyclostremiscus beaui.—Moore, 1964:131–135.—Morris, 1973: 138, pl. 40, fig. 19.—Porter, 1974:143.—Emerson & Jacobson, 1976:64, pl. 18, fig. 21.—Abbott & Dance, 1982: 58, text-fig.

Cyclostremiscus (Ponocyclus) beaui.—Warmke & Abbott, 1961: 60, pl. 11, fig. b.—Humfrey, 1975:76, pl. 3, figs. 11–11a.

Cyclostremiscus (Ponocyclus) beauii.—Abbott, 1974:85, text-fig. 786.—Rios, 1975:38, pl. 10, fig. 131; 1985:41, pl. 16, fig. 177.—Vokes & Vokes, 1983:15, pl. 25, figs. 4–4a.

Material examined: Lectotype (designated herein): 10.5 mm, MNHN unnumbered (Guadeloupe). Neotype of *Cyclostrema bicarinata*: 7.4 mm, USNM 115621 (Pliocene, Jamaica); other material: 60 specimens: NORTH CAROLINA: 1 specimen with dried animal, BEVERIDGE Sta. I (ex *Astropecten*), UNC-IMS. FLORIDA: Ft. Pierce Inlet: 10 March 1987, 1 male, 3 unsexed; 2–3 May 1987, 1 male; 24 June 1987, 3 males; 3 August 1987, 6 males; 31 August 1987, 7 females, 11 males; 14 September 1987, 1 female; 27 September 1987, 3 females, 2 males. Peanut Island, Lake Worth Inlet: 11 August 1987, 1 female, 1 male. Boynton Beach: 1 shell, ANSP 277740. Miami: 1 shell, EOLIS Sta. 311, USNM 449192. Fowey Light: 2 shells, EOLIS Sta. 187, USNM 449193; 1 shell, EOLIS Sta. 129, USNM 449194; 1 shell, EOLIS Sta. 142, USNM 449195; 1 shell, EOLIS Sta. 170, USNM 449196; 1 shell, EOLIS Sta. 355, USNM 449198. Turtle Harbor: 2 shells, EOLIS Sta. 61, USNM 449197. Sand Key: 1 shell, EOLIS Sta. 162, USNM 449199. Key West: 1 shell, EOLIS Sta. 63, USNM 449200. Dry Tortugas: 1 shell, USNM 61114; 1 shell, USNM 271949. Cape San Blas: 1 shell, USBF Sta. 2402, USNM 323914. CARIBBEAN: St. Martin: 1 shell, ANSP 20621. Jamaica: 1 shell, USNM 426872; 1 shell, USNM 442372. SOUTH AMERICA: Coveñas, Colombia: 1 shell, USNM 364409.

DESCRIPTION

Teleoconch (figures 1–3): Shell large for family [usually 2–3 whorls, 6–8 mm diameter ($\bar{x} = 6.9$, n = 56); height: $\bar{x} = 3.8$, n = 33; umbilical diameter: $\bar{x} = 1.5$, n = 30; largest specimen (female): diameter 11.5 mm, height 6.2 mm, umbilicus diameter 2.4 mm, teleoconch whorls 3⅜], nearly planispiral. Opaque-whitish, with 5–8 strong, concentric ribs on apical side, above peripheral keel. Widely-spaced irregular pustules between ribs (figures

Table 1. Anatomical characters and character states, and habitat types of species in the vitrinellid-tornid complex.

1) Projecting snout bilobed, lateral extensions: (a) absent; (b) present.
2) Cilia along cephalic tentacles: (a) absent; (b) present.
3) Terminal stiff setae on cephalic tentacles: (a) absent; (b) present.
4) Number of pallial tentacles.
5) Pallial tentacles: (a) all finger-shaped; (b) upper finger-shaped and lower paddle-shaped.
6) Upper pallial tentacle: (a) naked; (b) with motile cilia; (c) with stiff setae; (d) with distinct motile cilia and/or stiff setae.
7) Lower pallial tentacle: (a) naked; (b) with motile cilia; (c) with stiff setae; (d) with distinct motile cilia and/or stiff setae.
8) Gill filaments: (a) projecting from aperture in crawling position; (b) not projecting from aperture in crawling position.
9) Anterior foot margin: (a) straight or only weakly indented; (b) cleft.
10) Posterior foot margin: (a) simple and rounded or weakly indented; (b) cleft.
11) Operculum nucleus: (a) concentric; (b) subcentral.
12) Number of whorls on operculum.
13) Eyes: (a) distinctly developed; (b) lack nerve supply.
14) Osphradium: (a) small, ciliated groove; (b) distinctly developed, paralleling ctenidium.
15) Penis: (a) simple, without glandular processes, recurved; (b) with glandular area, directed straight back; (c) with several, finger-like processes.
16) Habitat: (a) under rocks; (b) under scales of annelid *Polyodontes lupina* (Stimpson); (c) ? from stomach of starfish; (d) in burrows of stomatopod *Lysiosquilla scabricauda* (Lamarck); (e) sandy mud bottom; (f) under large boulders on well-oxygenated sandy mud.

5–8) on first whorl, becoming more dense and regularly spaced on second whorl. Fields of pustules on body whorl intersected by smaller concentric ridges, 4–6 between major ribs, added first between suture and first major rib, subsequently between peripheral ribs. Strong cords forming sharp peripheral and basal keels, separated by wide flat area, inclined ventrally and marked by growth lines, spiral cords, and pustules. Base widely umbilicate, with 0–5 concentric ribs between basal keel and umbilicus; larger specimens showing decreasing number of ribs with increasing size. Umbilical wall often with 2–4 narrow ribs. Outer lip sinuous, with shallow sutural sinus. Microstructure (figure 4) of 3 layers: 2 thick cross-lamellar layers and 1 thin homogenous outer layer thickened to form spiral ribs.

Protoconch (figures 9–11): Diameter 0.40–0.48 mm ($\bar{x} = 0.45$, n = 32). Protoconch I (prior to hatching) smooth, of about 1 whorl (diameter $\approx$ 0.23 mm). Protoconch II (after hatching, before settling) of an additional whorl, sculptured with irregular, more-or-less concentric markings (figure 11). Total protoconch of 2 whorls, rather high-spired (spire angle $\approx$ 50°).

Table 2. Summary of anatomical and habitat data for species in the vitrinellid-tornid complex. Characters and character states are listed in table 1. Sources of data listed under each species. ** = type species of genus; * = synonym of type species of genus. *· = c according to Moore, 1964:22; d according to Moore, 1964:159. All biological data from Florida, except for *Cochliolepis parasitica* (also South Carolina), *Co. albicerata* (New Zealand), *Circulus striatus* Guernsey, English Channel).

Species	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Group 1																
**Vitrinella helicoidea* C. B. Adams, 1850																
Pilsbry & McGinty, 1945a: pl. 2, fig. 5; 1946b:13	a	b	b	2	a	d	a	a	a	a	?	?	a	?	?	a
Vitrinella praecox Pilsbry & McGinty, 1946																
Pilsbry & McGinty, 1945a: pl. 2, fig. 4; 1946b:14	a	b	b	2	a	a	d	a	a	a	?	?	a	?	?	?
Teinostoma carinacallus Pilsbry & McGinty, 1946																
Pilsbry & McGinty, 1946b:17, pl. 2, fig. 6b.	a	b	b	2	a	d	a	a	a	a	?	?	?	?	?	a
Teinostoma lerema Pilsbry & McGinty, 1945																
Pilsbry & McGinty, 1945a:6, pl. 2, fig. 1a.	a	b	b	2	a?	d	?	a	a	?	?	?	?	?	?	a
Teinostoma parvicallum Pilsbry & McGinty, 1945																
Pilsbry & McGinty, 1945a:4, pl. 2, fig. 2.	a	b	b	2	a	d	d	a	a	a	?	?	?	?	?	a
***Pleuromalaxis balesi* (Pilsbry & McGinty, 1945)																
Pilsbry & McGinty, 1945a:10, pl. 2, fig. 8.	a	b	b	2	a	d	a	a	a	?	?	?	?	?	?	a
***Cochliolepis parasitica* Stimpson, 1858																
Stimpson, 1858:307ff.; Moore, 1972:100ff.	a	a	b	2	a	a	b	a	a	a	a	?	a	?	a	b
Cochliolepis albicerata Ponder, 1966																
Ponder, 1966:38, pl. 5.	a	b	b	1	a	—a—	b	a	a	a	6	a	?	?	a
Circulus striatus (Philippi, 1836)																
Fretter, 1956:369ff.; Fretter & Graham, 1978:227ff.	a	a	b	2	a	c	c	b	a	a	a	12	a	b	a	c
Circulus texanus (Moore, 1965)																
This paper.	a	b	b	2	a	c	b	a	a	a	a	8	a	b	a	d
Cyclostremiscus beauii (Fischer, 1857)																
This paper.	a	b	b	2	b	c	b	a	a	a	a	7	a	b	a	d
Cyclostremiscus pentagonus (Gabb, 1873)																
Bush, 1897:127, pl. 22, figs. 6, 12a–g [as *Skenea trilix*].	a	?	?	?	?	?	?	?	?	?	a	5	a	?	?	e
Group 2																
***Tomura bicaudata* (Pilsbry & McGinty, 1946)																
Pilsbry & McGinty, 1945a: pl. 2, fig. 9; 1946b:15.	b	a	a	1	a	—a—	b	b	b	b	?	?	?	?	a
**Parviturboides interruptus* (C. B. Adams, 1850)																
Moore, 1962:695ff., fig. 1B; 1964:21, 156ff.;																
1972:106ff., figs. 5, 6.	a	b	b	2	a	*¹	d	b	a	b	a	?	a	?	b	a
Group 3																
***Tornus subcarinatus* (Montagu, 1803)																
Woodward, 1898:140ff., pl. 8, figs. 1–3, 5–7; Fretter &																
Graham, 1978:229ff.; Graham, 1982:144ff.	a	b	b	2	a	a	a	a	a	b	?	b	a	c	f

External anatomy and organs of the mantle cavity (figures 12–18, 20–25, 27, 34–37): Living animal translucent yellowish-orange, with buccal mass, anteriormost gill filaments, and tip of penis rose-pink; digestive gland brownish-orange. Base of ctenidial lamellae on osphradial side pigmented white; central area of osphradium white flanked by brown lines on each side, resulting in pattern of parallel lines on left body side (figure 12). Long snout terminating in pair of muscular "lips," separated by vertical slit with mouth opening. Lips separated from remainder of snout by strongly ciliated groove. Serial sections revealed 2 narrow longitudinal bands of cilia, situated in grooves on each side, beginning shortly behind tip of snout. Two slender, flexible, cephalic tentacles reaching approximately twice length of snout when fully extended. Left tentacle fitting into shallow notch formed by ventral shell keel (figure 14). Black eyes on outer expanded bases of cephalic tentacles, each equipped with spherical, transparent lens.

Cephalic tentacles exhibiting elaborate pattern of mo-

Figures 1–11. *Cyclostremiscus beauii*, specimens from Ft. Pierce Inlet, Florida (SEM) (figures 1–3, USNM 846323). **1.** Shell, apical view (8.0 mm diameter). **2.** Shell, umbilical view (5.0 mm diameter). **3.** Shell, apertural view (4.1 mm diameter). **4.** Microstructure of lateral body wall, fracture surface parallel to growing edge. **5.** Teleoconch sculpture, apical view. Circled numbers indicate location of sculptural details in figures 6–8. Stars indicate location of sutures. **6.** Detail of teleoconch sculpture, first whorl. **7.** Detail of teleoconch sculpture, second whorl. **8.** Detail of teleoconch sculpture, third (= body) whorl. **9.** Protoconch, apical view. Arrow indicates sculptural line between protoconchs I and II. **10.** Protoconch, lateral view. **11.** Sculpture of protoconch I (left, smooth) and protoconch II (right, sculptured). Scale bars: 4, 5, 8–10 = 0.1 mm; 6, 7, 11 = 10 μm.
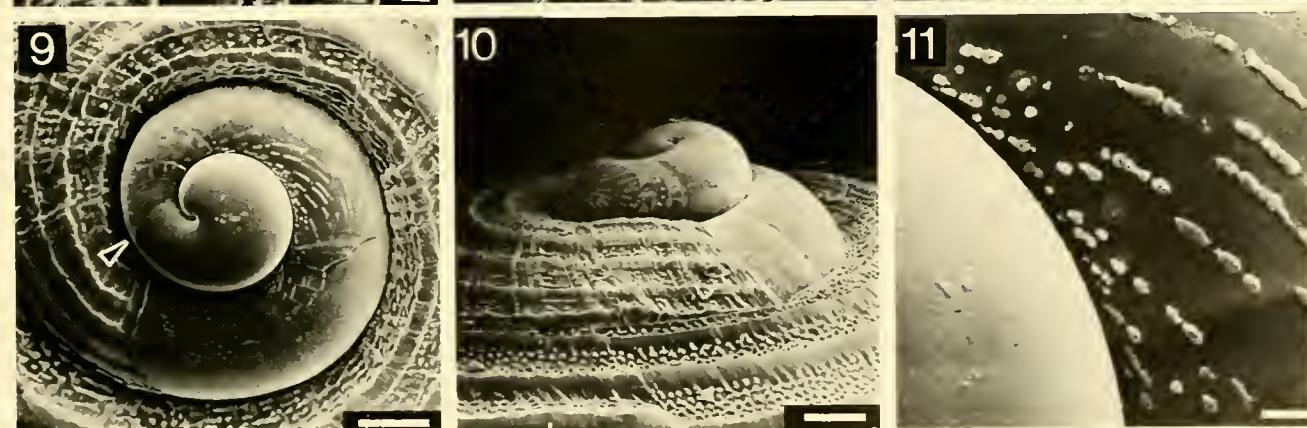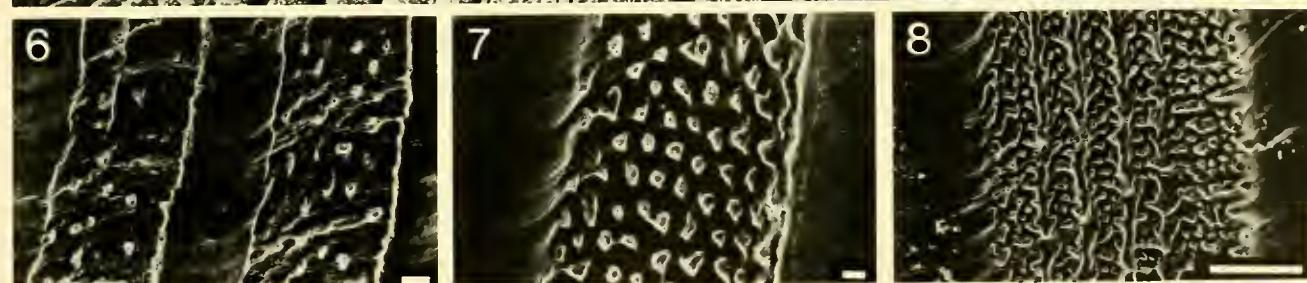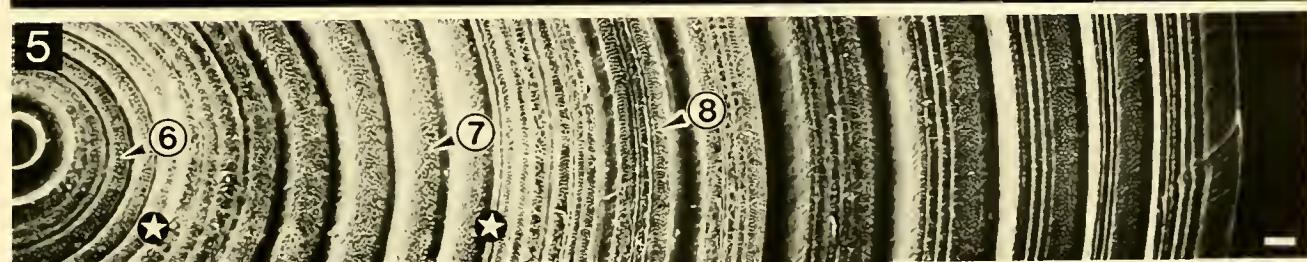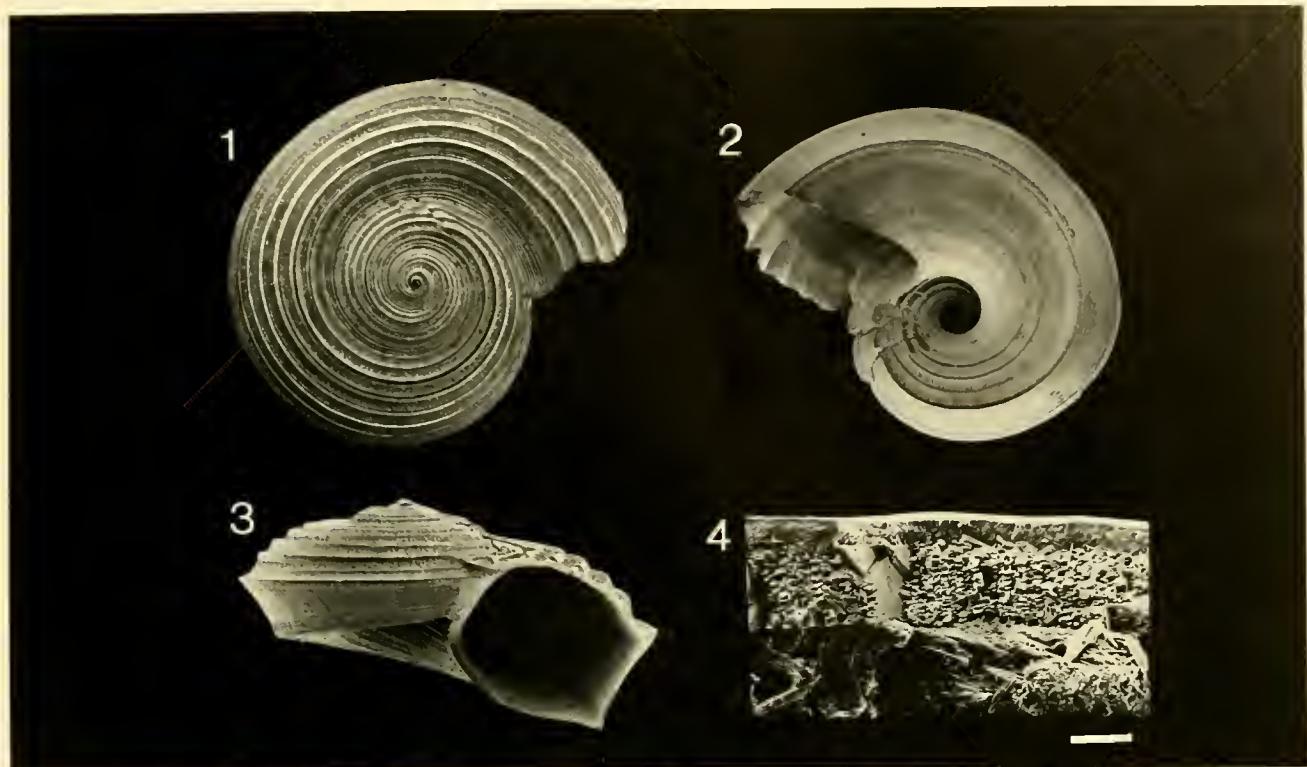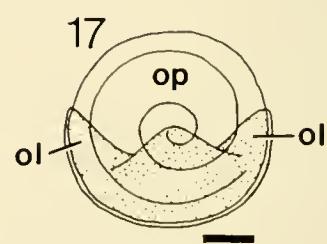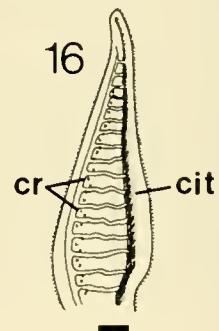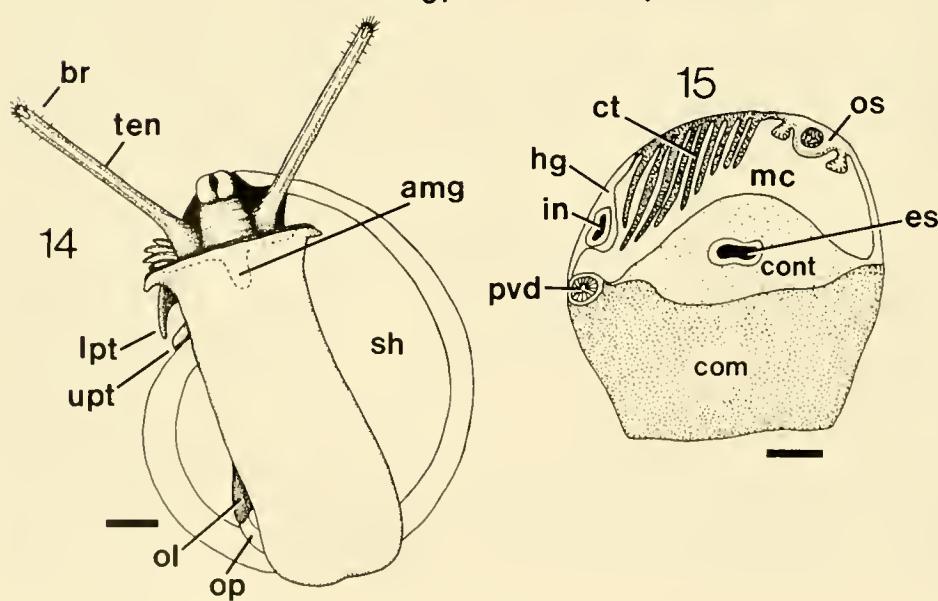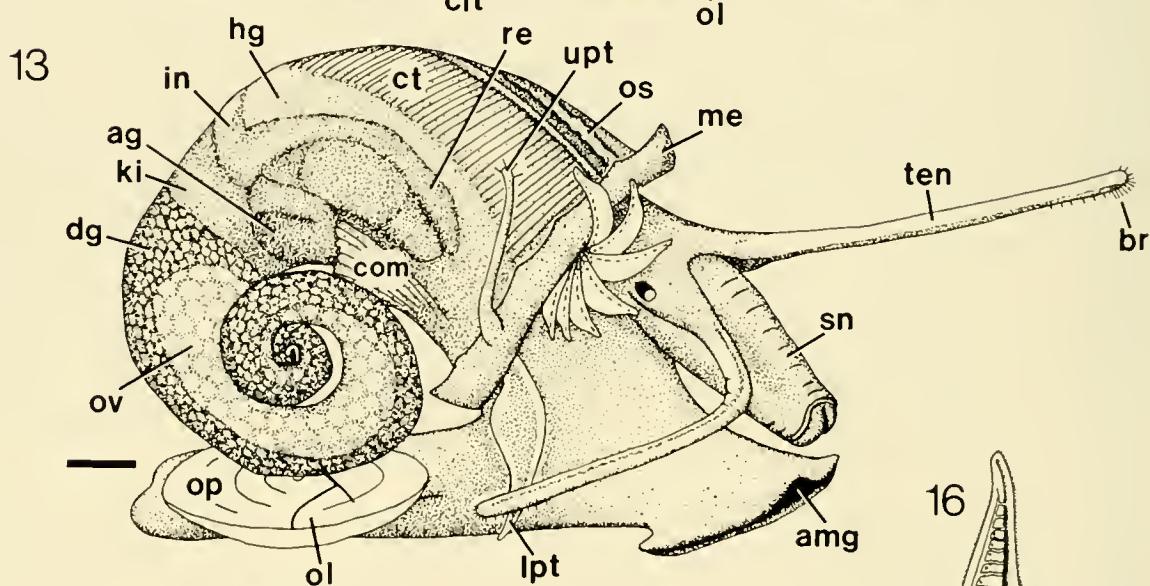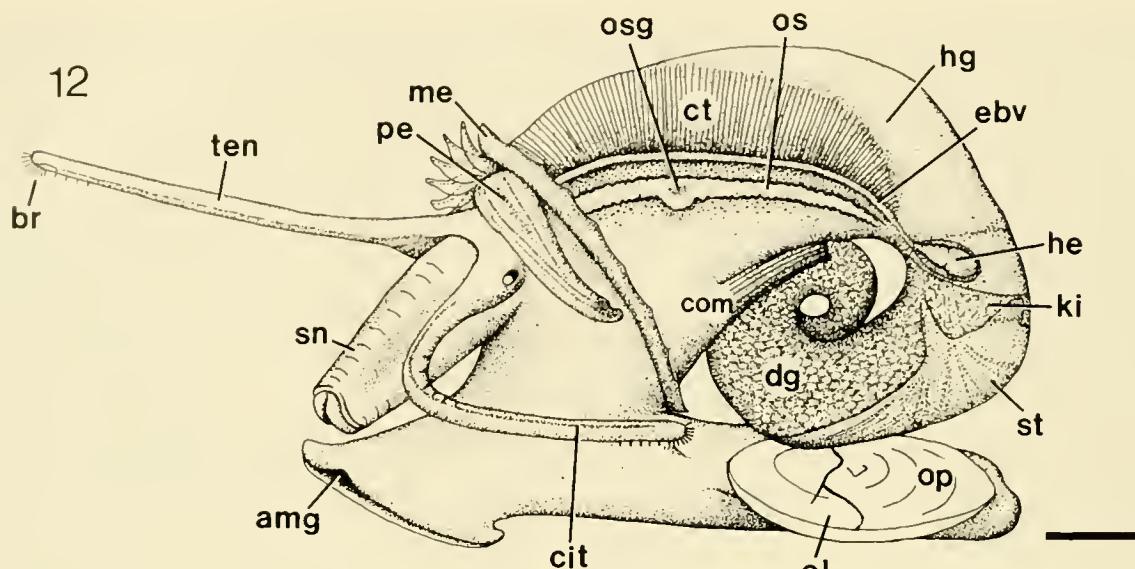
tile cilia and stiff bristles. Ventral tip of each tentacle with U-shaped, heavily-ciliated groove surrounding smooth area, forming tactile pad (figure 25, tp). Numerous stiff bristles (lost during fixation, therefore not evident in histological or SEM preparations) distal to and just behind pad; additional bristles sparsely distributed over distal quarter of tentacle. Two longitudinal ciliated tracts, situated in grooves, extending from region of pad on ventral side. Near tentacle base, innermost groove sloping dorsally toward dorsal midline; outermost groove ending proximal to expanded tentacle base (figure 20). Flattened base of tentacle facing snout surface covered by additional, irregular, parallel tracts of cilia (figure 20). Third longitudinal ciliated groove on dorsal side of tentacle extending from flattened, triangular area just below eye to near tentacle tip (figure 18). Ciliated grooves usually lined by narrow bands of brown pigment. Cilia fully retractable into grooves. Cilia in grooves with distinct movement pattern (right tentacle: dorsal row—toward tentacle base, inner and outer ventral rows—toward tip; left tentacle: opposite directions). (These movements are easily mistaken for direction of ciliary beating, and therefore current flow. However, further microscopic observation with the aid of carmine and fluorescein sodium particles revealed lateral beating of the individual cilia across the tentacle, away from the snout, indicating that the apparent ciliary movement actually reflects the conduction of nervous impulses along the tentacle.) In cross-section, each tentacle usually with 3 nerves, 1 larger blood sinus, and several smaller blood spaces in central area, especially around nerve cords (figure 24).

Foot (figures 12–14) elongate (just reaching posterior shell margin in crawling animal), flattened, densely and finely ciliated, with anterolaterally recurved corners; broadly rounded posteriorly and slightly indented at posterior terminus. Anterior pedal mucous gland (figure 14, amg) present, opening at center of transverse slit across anterior, leading edge of foot. No posterior mucous gland or metapodial tentacles. Locomotion by ciliary action.

Operculum (figures 17, 34–37) corneous, circular, multispiral, with about 7 whorls and small internal knob, supported by finely ciliated opercular lobes (figure 17, ol) on dorsal side of foot. Lobes simple, unpigmented, without tentacles. Lemon-shaped muscle scar on internal surface of operculum (figure 35).

Mantle edge (figures 12, 13) somewhat scalloped, corresponding to spiral ribs of shell. Large monopectinate ctenidium, attached along entire length to inner surface of mantle, originating on posterior left, curving over dorsum, terminating just above right eye where last few gill filaments protrude from aperture. Numerous (≤ 180) gill filaments (figures 16, 21) flattened, elongated leaflets, almost finger-like when contracted, forming tapered blades when extended. Filaments longest in central part of gill, decreasing somewhat in size toward both ends. "Supporting rods" lacking; filaments well supplied with blood spaces and muscles (transverse muscle bands giving extended filaments ladder-like appearance; figure 16). Both sides of blade carrying wide band of cilia off-center, closer to left (osphradial) side. Along right side in same relative position, each filament with longitudinal row of small embedded crystals (figure 16, cr). Narrow rim clear, somewhat thinner on "crystal" side, bearing continuous band of cilia. Filaments draining into large efferent branchial vessel leading to heart (figure 12). Filaments hardly reacted to direct physical stimuli, contracting rapidly when either cephalic tentacle or finger-shaped pallial tentacle (see below) touched.

Whitish hypobranchial gland (figures 12, 13) paralleling entire length of rectum, most conspicuous posteriorly. Osphradium (figures 12, 22, 23) paralleling almost entire left side of gill, comprised of wide central area and two strongly developed, heavily ciliated, lateral zones. Central area with irregular chevron-like pattern of tracts of shorter cilia. Osphradial ganglion (figure 12, osg) very conspicuous at point about ⅓ of total length from mantle edge. Mantle cavity ending immediately behind posterior end of ctenidium.

Two pallial tentacles (figures 13, 27) arising from just inside right mantle edge; upper (= most dorsal) tentacle finger-shaped, unciliated, somewhat closer to mantle edge, curling into shallow sutural sinus, directed dorsally. Lower tentacle paddle-shaped, ciliated at edges (except on narrow stalk) and also across its broad surface; narrow band at tentacle edge unciliated. Single stiff bristles sometimes occurring at tip. Lower tentacle originating at point on mantle edge ventral and slightly more interior to upper finger-shaped tentacle; directed anterolaterally. Stimulation with forceps or needle caused immediate contraction of upper tentacle (followed by contraction of cephalic tentacles and exposed ctenidial filaments). Lower tentacle showed little response to touch and cannot markedly contract (compare tentacles in figure 27). Lower tentacle observed to regulate and enhance water

Figures 12–17. *Cyclostremiscus beauii.* **12.** Male, left side, in crawling position (shell removed). Penis reflected anteriorly, out of mantle cavity. **13.** Female, right side, in crawling position (shell removed). Mantle slightly reflected to show relative insertion points of pallial tentacles. **14.** Crawling animal, ventral view. **15.** Diagrammatic cross-section through mantle cavity of male, at level of osphradial ganglion. **16.** Gill filament. **17.** Diagrammatic view of closed operculum, as seen when animal is retracted, showing position of opercular lobes. Scale bars: 12–14 = 1.0 mm; 15 = 0.5 mm; 16 = 0.1 mm.

ag, albumen gland; amg, anterior mucous gland; br, immobile bristles; cit, ciliary tract; com, columellar muscle; cont, connective tissue; cr, crystals; ct, ctenidium; dg, digestive gland; ebv, efferent branchial vessel; es, esophagus; he, heart; hg, hypobranchial gland; in, intestine; ki, kidney; lpt, lower pallial tentacle; mc, mantle cavity; me, mantle edge; ol, opercular lobe; op, operculum; os, osphradium; osg, osphradial ganglion; ov, ovary; pe, penis; pvd, pallial vas deferens; re, rectum; sh, shell; sn, snout; st, stomach; ten, cephalic tentacle; upt, upper pallial tentacle.
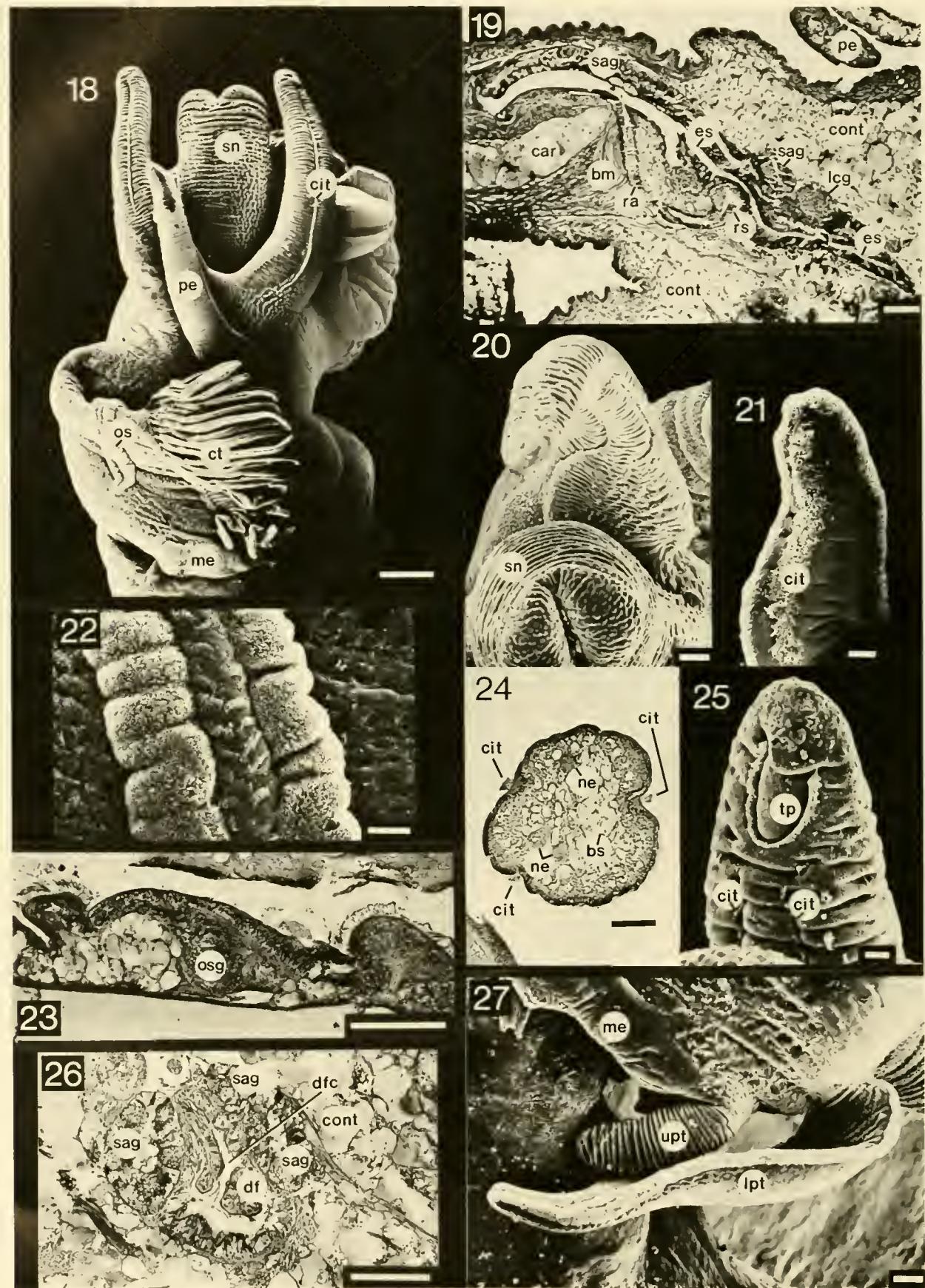
flow, by paddle positioning and by strong ciliary action, respectively, in or out of right side of mantle cavity.

Alimentary system: Mouth opening between pair of muscular lips into large buccal mass (figure 42; length 1.3 mm in specimen 8.5 mm shell diameter). Radula protruding from short radular sac (figure 42, ras) extending somewhat behind and to left of buccal mass.

Paired jaws (figure 41) each crescent-shaped, approximately 0.5×0.16 mm (in specimen 7.8 mm shell diameter), composed of interlocking diamond-shaped elements 14 μm in length, varying slightly in shape across surface of jaw.

Radula (figures 28–33) taenioglossate, with about 100 rows (max. 138; n = 7), length $\approx$ 1.3 mm, width $\approx$ 0.2 mm. Rachidian tooth (figure 31) wider than long (0.40 μm wide, n = 8), with acute posterior corners projecting laterally, and concave front. Main cusp narrowly-triangular, unserrated, with 4–5 flanking cusps on each side (number of flanking cusps varying within single radula, apparently by splitting and fusion), decreasing laterally in size; base with 1 strong basal denticle per side, midway between posterior corners and central ridge. Lateral tooth (figures 32, 33) with asymmetrical cutting edge, strongly indented at front edge, bearing large, narrowly-triangular, unserrated main cusp and highly variable number of flanking cusps (3–6 inner, 7–8 outer) decreasing in size laterally. Base of lateral tooth with broad central ridge; basal platform long, blade-like. Apex of inner marginal (figures 30, 33) with short, stout main cusp, and 12–14 subequal, inner and outer flanking cusps. Stalk long, blade-like, with robust supporting ridge. Apex of outer marginal (figures 28, 30) with sharp, undulating inner margin (sometimes finely incised into closely-adhering flanking cusps), and smooth, rounded outer margin.

Esophagus opening widely into buccal cavity, without esophageal pouches. Salivary glands (figures 19, 26, 42) narrow, tube-like, emptying into buccal mass at its lateral mid-point, extending posteriorly along esophagus. Position of salivary ducts relative to circumesophageal nerve ring highly variable: some or all passing through ring (n = 3; figure 49), stopping just anterior to ring (n = 4), or extending past without going through ring (n = 2). Relative lengths of salivary glands vary. Anterior part of esophagus, in cross-section (figures 26, 43), bearing 2 muscular, longitudinal, dorsal folds, their lower extensions coiling upwards to form semi-isolated compartments. Anterior esophagus thus divided into strongly ciliated dorsal food channel (figure 26, dfc), larger ventral channel, and two small lateral pockets. Posterior to nerve ring (figure 42), ventral projections into main channel increasing gradually in size, but without clear distinction between anterior and mid-esophageal regions. Food channel remaining dorsal. Dorsal folds and ventral projections gradually decreasing in size, with posterior esophagus as a simple muscular tube.

Stomach (figures 12, 38–40) amber in color, slightly translucent in living animal, approximately 4×1.5 mm (in largest specimen, 11.5 mm shell diameter), lying on exterior surface of visceral coil, appressed to the surface of digestive gland just posterior to heart and kidney, encompassing approximately ½ total length of digestive gland. Stomach consisting of two continuous chambers (figure 39) differing in function: anterior chamber (⅓ of total stomach length) containing gastric shield, working end of crystalline style, and all openings into stomach; remaining ⅔ forming large sorting and storage chamber.

Esophagus entering stomach on left side at junction of anterior and posterior chambers. From this point, series of folds extending transversely across stomach, posteriorly into posterior chamber, and anteriorly toward intestinal opening. Opening to digestive gland lying to right of esophageal opening, between it and gastric shield. Gastric shield (figures 39, 40), with cup-like lateral wing upon which crystalline style rotates, protruding into anterior chamber, and central longitudinal portion with flattened lateral expansion that cradles style, positioning it against cup-like grinding surface.

Style sac and intestine, at anterior end of stomach, usually partially obscured by connective tissue and kidney. Style sac (figure 39, ss) narrow, finger-shaped, approximately ⅓ length of stomach, not communicating directly with intestine [Johansson's (1940:1) group 3, revised after Mackintosh (1925)]. Style completely transparent, rod-shaped (length 1.8 mm, diameter 0.35 mm), rotating within style sac by action of densely packed cilia on style sac walls, protruding into anterior chamber of stomach through fleshy tube-like structure above gastric shield. Channel extending between digestive gland opening and intestinal opening at anterior terminus of anterior chamber.

Figures 18–27. *Cyclostremiscus beauii*, specimens from Ft. Pierce Inlet, Florida (light micrographs or critical-point dried SEM preparations). **18.** Head-foot (male), with mantle edge reflected posteriorly, dorsal view (SEM). **19.** Sagittal section of male through buccal mass and esophageal region. **20.** Anterior view of snout and left cephalic tentacle, showing pattern of ciliated tracts on ventral surface (SEM). **21.** Tip of gill filament (SEM). **22.** Osphradium, anterior to osphradial ganglion (SEM). **23.** Osphradium, cross-section through osphradial ganglion. **24.** Cephalic tentacle, cross-section. **25.** Ventral tip of cephalic tentacle, showing tactile pad (SEM). **26.** Esophagus, cross-section through anterior section, with salivary glands. **27.** Pallial tentacles: upper, finger-shaped tentacle (retracted), and lower, paddle-shaped tentacle (SEM). Scale bars: 18 = 0.5 mm; 22 = 50 μm; 19, 20, 23, 24, 26, 27 = 0.1 mm; 21, 25 = 20 μm.

bm, buccal mass; bs, blood space; car, cartilage; cit, ciliary tract; cont, connective tissue; df, dorsal folds of esophagus; dfc, dorsal food channel of esophagus; es, esophagus; lcg, left cerebral ganglion; lpt, lower pallial tentacle; me, mantle edge; ne, nerve; os, osphradium; osg, osphradial ganglion; pe, penis; ra, radula; rs, receptaculum seminis; sag, salivary gland; sn, snout; tp, tactile pad; upt, upper pallial tentacle.
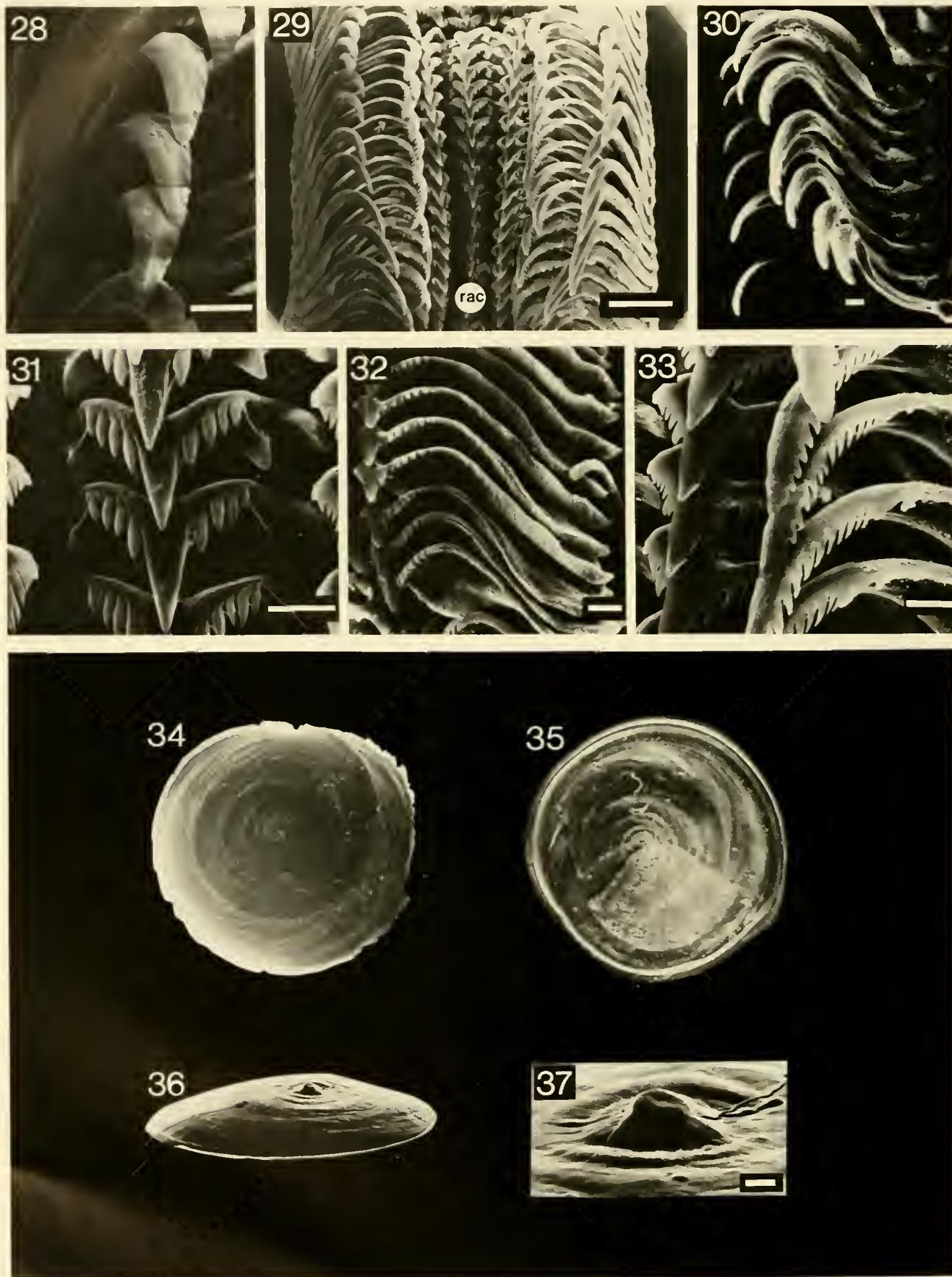
Posterior chamber (figures 39, 47, pch) with irregular longitudinal folds along its left side leading from esophageal opening, and well-defined longitudinal groove on its right side leading toward gastric shield. Central area with series of ciliated transverse folds.

Proximal portion of intestine (figure 39, in) consisting of 3 histologically separate sections: (1) slightly bulging section immediately adjacent to stomach, containing large typhlosole, leading into second section via small loop; (2) very muscular, ball-shaped section passing under style sac to join third section; and (3) moderately ridged intestine proper, initially quite narrow, dilating slightly as it passes, without further loops or undulations, toward rectum in mantle cavity. Anus set back from mantle edge. No special ciliated tracts from anus to mantle edge and exterior.

Observed flow of particles (figure 39, small arrows): Large and small food particles enter stomach through esophagus. Counter-clockwise whirlpool at esophageal opening preliminarily sorts particles according to size. Smaller particles pass laterally to right in groove toward gastric shield and style. Large particles move into posterior chamber along left series of longitudinal folds, passing to far posterior terminus of stomach. From there, particles pass into central area where peristaltic action manipulates and returns large particles to anterior chamber. Concurrently, smaller particles separate and/or break off, and follow transverse folds toward right longitudinal groove, and then anteriorly within groove toward gastric shield. Large particles in central area of sorting chamber continue moving anteriorly to region of esophageal opening, where they pass rapidly by ciliary action directly to intestinal opening. Small particles entering area of gastric shield are manipulated by clockwise-rotating style against cup-shaped flange of gastric shield. Resultant particles move directly left into opening of digestive gland, guided by cuticularized lateral folds near style sac opening. Unacceptable particles and material returning from digestive gland are shunted via longitudinal groove toward intestinal opening. Ball-shaped proximal section of intestine probably serves as a pellet compressor.

Live specimens fed on single-celled algae and detritus scraped from laboratory aquaria walls. Fecal pellets oval, 0.33 × 0.19 mm (n = 5), round in cross-section, with rounded ends.

Renopericardial system: Two-chambered heart and surrounding kidney visible on left surface of visceral coil, posterior to ctenidium and hypobranchial gland (figure 12). Kidney large, with nephridial gland on its outer wall.

Kidney opening at posteriormost end of mantle cavity, without conspicuous ciliated tract associated with opening. No gonopericardial or renogonadial ducts observed.

Nervous system: Circumesophageal ganglia (figures 42, 43, 49) moderately concentrated. RPG ratio [Davis *et al.*, 1976:263; defined as length of pleurosupraesophageal connective/(length of connective + length of right pleural ganglion + length of supraesophageal ganglion)] averaged 0.49 (n = 7). Cerebral ganglia connected by narrow commissure, each separated from pleural ganglia by constriction. Tentacular nerves with distinct swellings at their bases. Pedal ganglia each with paired connectives, connecting anteriorly to cerebral ganglia, posteriorly to cerebropleural junctions. Pedal commissure very short, narrow. Subesophageal ganglion somewhat smaller than supraesophageal ganglion; connective to its pleural ganglion much shorter. Statocysts (figure 44, stc) about 110 μm diameter. Buccal ganglia small, conspicuous, joined by commissure passing beneath esophagus at posterior end of buccal mass.

Highly-vacuoled connective tissue surrounding nerve ring, as well as other organs and areas throughout body.

Reproductive system: Animals in male phase (for discussion of sex change, see below) distinguished from functional females by smaller size and by dark-orange, rather than creamy-orange or beige, gonadial coloration. Penis large (size at rest: length 2.5–3.0 mm, width at midlength 0.4 mm), muscular, somewhat flattened (figures 12, 18, 42, 44) arising just behind and slightly right of bases of cephalic tentacles, coiling counter-clockwise back into mantle cavity. Fully extended penis may be longer than cephalic tentacles (*e.g.*, 4.4 mm *vs.* 3.0 mm). Subcentral penial duct terminating in opening on slightly hooded tip, which, unlike remainder of penis, is unciliated. Long, closed pallial vas deferens extending from penis, along right side of body, to prostate in posterior part of mantle cavity (figure 44). Vas deferens relatively wide (diameter ≈ 0.2 mm), tubular, forming prominent, somewhat undulating ridge that differs from surrounding tissue by its shiny, unciliated surface and by its white appearance caused by heavy internal ciliary action. Prostate orange, egg-shaped, 0.65–0.90 × 0.35–0.48 mm (n = 5), lying ventral to rectum, connected to right pallial wall, its lumen communicating with mantle cavity by slit (≈ 0.35 mm length) at its base (figures 44, 48). Visceral vas deferens much narrower, passing through posterior mantle wall, leading along inner coil of visceral mass, where widened, extensively-coiled portion functions as vesicular seminalis (figure 47, vs) before reaching

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Figures 28–37. *Cyclostremiscus beauii*, radula and operculum, specimens from Ft. Pierce Inlet, Florida (SEM). **28.** Outer marginal teeth. **29.** Radula, whole mount. **30.** Inner marginal teeth. **31.** Rachidian teeth. **32.** Lateral teeth. **33.** Tips of lateral (left) and inner marginal (right) teeth. **34.** Operculum, outer surface (2.1 mm diameter). **35.** Operculum, inner surface (1.7 mm diameter). **36.** Operculum, oblique lateral view of inner side (2.2 mm diameter). **37.** Opercular peg, oblique lateral view. Scale bars: 28, 30–33 = 10 μm; 29, 37 = 50 μm.

rac, rachidian teeth.
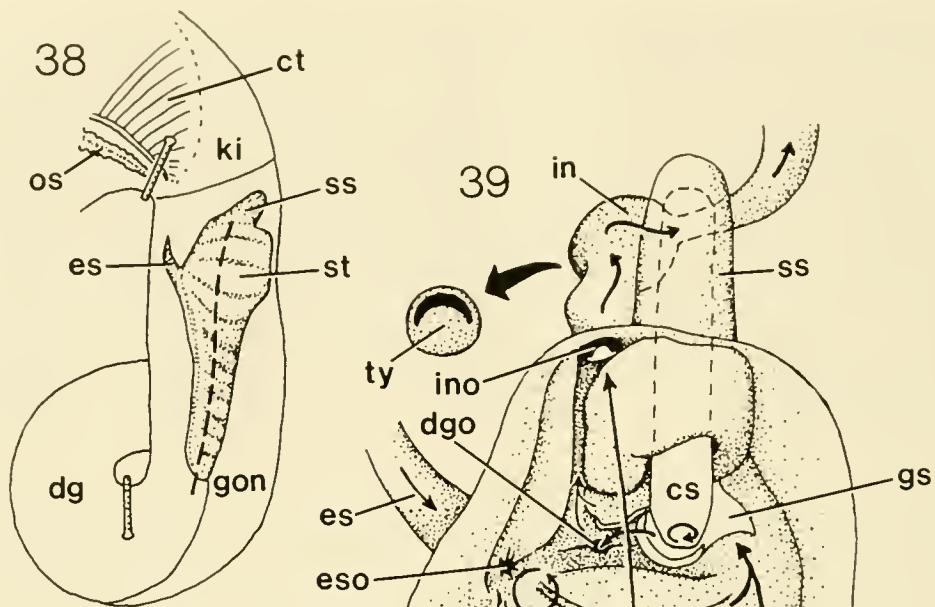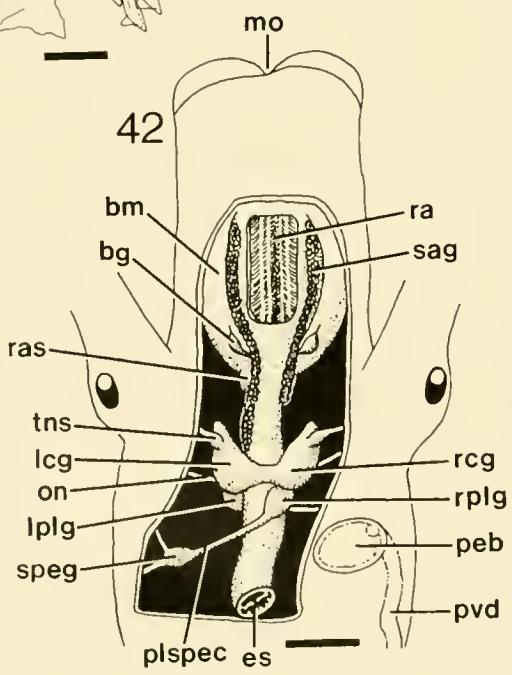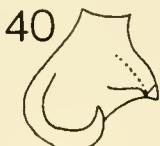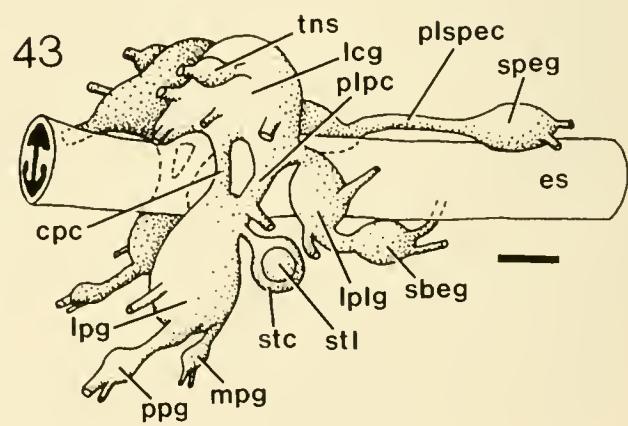
testis. Testis simple, elongated sac, yellow to bright orange, along inner right side of visceral coil, totalling 50–60% of its length (figure 44).

Spermatozoon (56–62 μm total length, n = 3) with slightly twisted head comprising elongated nucleus and pointed acrosome (≈ 14% of total length), very long, narrow midpiece (≈ 58%) and long tail (≈ 28%). Atypical sperm not found.

Female reproductive tract (figures 13, 46) adjacent to rectum along right side of mantle cavity. Female opening, about level with anus, situated on muscular papilla hanging freely in mantle cavity at distal end of capsule gland. From there, closed sperm duct leading posteriorly, initially forming very thick-walled muscular vagina (figure 52), with lumen almost filled with large gland cells. Sperm duct giving rise to small, ball-shaped, dorsally-situated sperm pouch with weakly muscular walls. Thin-walled ducts leading from sperm pouch and muscular vagina joining shortly before opening into slit-like lumen of massive capsule gland. Vagina-type muscular wall gradually disappearing, while thin-walled part forms sperm channel ("sperm groove" in "ventral channel" of authors), in communication with gland but partially separated by lateral fold (figure 46, cross-section B, lf). Anterior part of capsule gland with large, turquoise-staining gland cells; remaining capsule gland staining dark blue in sections. [At least in the anterior part, the gland cells are arranged in a complex pattern (see Ponder, in press). A detailed histological description was hampered by the extremely strong staining reaction of the glands.] Posteriorly, glandular mass continuing, with communicating lumina, as albumen gland. Albumen gland massive, thick-walled, with narrow, slit-like lumen, pinkish-orange in living animals, staining turquoise in sections; folded as S-shaped loop on right side of animal, partly in parallel with posterior part of capsule gland. Posteriormost part of albumen gland pressing against, or, in large females, extending beyond posterior mantle wall. Sperm channel separating at junction of capsule and albumen glands, forming closed oviduct, penetrating posterior mantle wall, and forming large, widened, non-glandular coil, containing (from sections and dissected specimens) both sperm and eggs. At its posterior end, coiled oviduct giving rise to 2 proximal sperm pouches, as inconspicuous, subequal, ball-shaped sacs, closely adjacent, and partially hidden under layers of connective tissue and kidney.

In ripe females, unoriented sperm, often in large quantities, found throughout length of sperm channel and in anterior sperm pouch (functional bursa copulatrix). Packed oriented sperm, with heads embedded in walls, found in the two posterior pouches (receptacula seminis).

Visceral oviduct very thin-walled, leading from coiled oviduct to ovary. Ovary situated at right side of visceral mass, structure not grape-like, extending over central 80% of digestive gland, covering half to all of right side of coil (figure 46).

(During copulation, sperm are apparently deposited in the vagina, temporarily stored in the bursa copulatrix and then stored in the two posterior receptacula. Fertilization occurs in the anterior part of the coiled oviduct, after which fertilized eggs pass through the ciliated lumina of the albumen and capsule glands where they are surrounded by capsular and mucous material. Eggs apparently enter the mantle cavity through the vagina, as no other female opening was found.)

Sex and size relationships (figure 53): Specimens less than 7.6 mm shell diameter (n = 25) were all males. Specimens of shell diameter greater than 8.6 mm (n = 6) were all fully functional females without male reproductive structures. Specimens 7.8–8.5 mm shell diameter (n = 6) were "transitional" in appearance (figure 45); visceral and pallial reproductive organs were clearly female, however, with visible remnant of pallial vas deferens and "wound" (= penis scar) at attachment site of penis. Pallial vas deferens of smallest "transitional" specimen present as unciliated duct, partially opened at proximal end, extending between penis scar and distal end of capsule gland. No positive connections observed. This specimen also with nearly transparent gonad containing small amount of whitish ovarian tissue in early part of coil, and with no sperm in the female system (it apparently had not yet mated in its female phase). Largest "transitional" specimen with fully-developed ovary, faint longitudinal marking on integument in position of vas deferens, and weak penis scar. Simultaneous possession of both ovarian and testicular tissues not observed.

"Transition" somewhat correlated with date of collection (figure 53). Collections made between March and mid-August exclusively male. Fully developed females, "transitional" individuals, and males encountered in each of four collections in later part of August and September.

Figures 38–43. *Cyclostremiscus beauii.* **38.** Left lateral view of visceral coil, showing position of stomach. Dashed line indicates location of dorsal incision. **39.** Stomach, dorsal view, opened at incision shown in figure 38. Arrows inside stomach indicate flow of particles. **40.** Gastric shield. **41.** Right jaw, inner side, posterior end up, showing details of jaw elements. **42.** Head with mid-dorsal incision showing buccal mass, circumesophageal nerve ring, and base of penis. Connective tissue and minor nerves removed **43.** Central nervous system, left side, oblique lateral view. Scale bars: 39, 42 = 0.5 mm; 41, 43 = 0.1 mm.

bg, buccal ganglion; bm, buccal mass; cpc, cerebropedal connective; cs, crystalline style; ct, ctenidium; dg, digestive gland; dgo, opening of digestive gland; es, esophagus; eso, opening of esophagus; gon, gonad; gs, gastric shield; in, intestine; ino, opening of intestine; ki, kidney; lcg, left cerebral ganglion; lplg, left pleural ganglion; lpg, left pedal ganglion; mo, mouth; mpg, metapodial ganglion; on, optic nerve; os, osphradium; pch, posterior chamber; peb, base of penis; plpc, pleuropedal connective; plspec, pleurosupraesophageal connective; ppg, propodial ganglion; pvd, pallial vas deferens; ra, radula; ras, radular sac; rcg, right cerebral ganglion; rplg, right pleural ganglion; sag, salivary gland; sbeg, subesophageal ganglion; speg, supraesophageal ganglion; ss, style sac; st, stomach; stc, statocyst; stl, statolith; tns, swelling of tentacular nerve; ty, typhlosole.
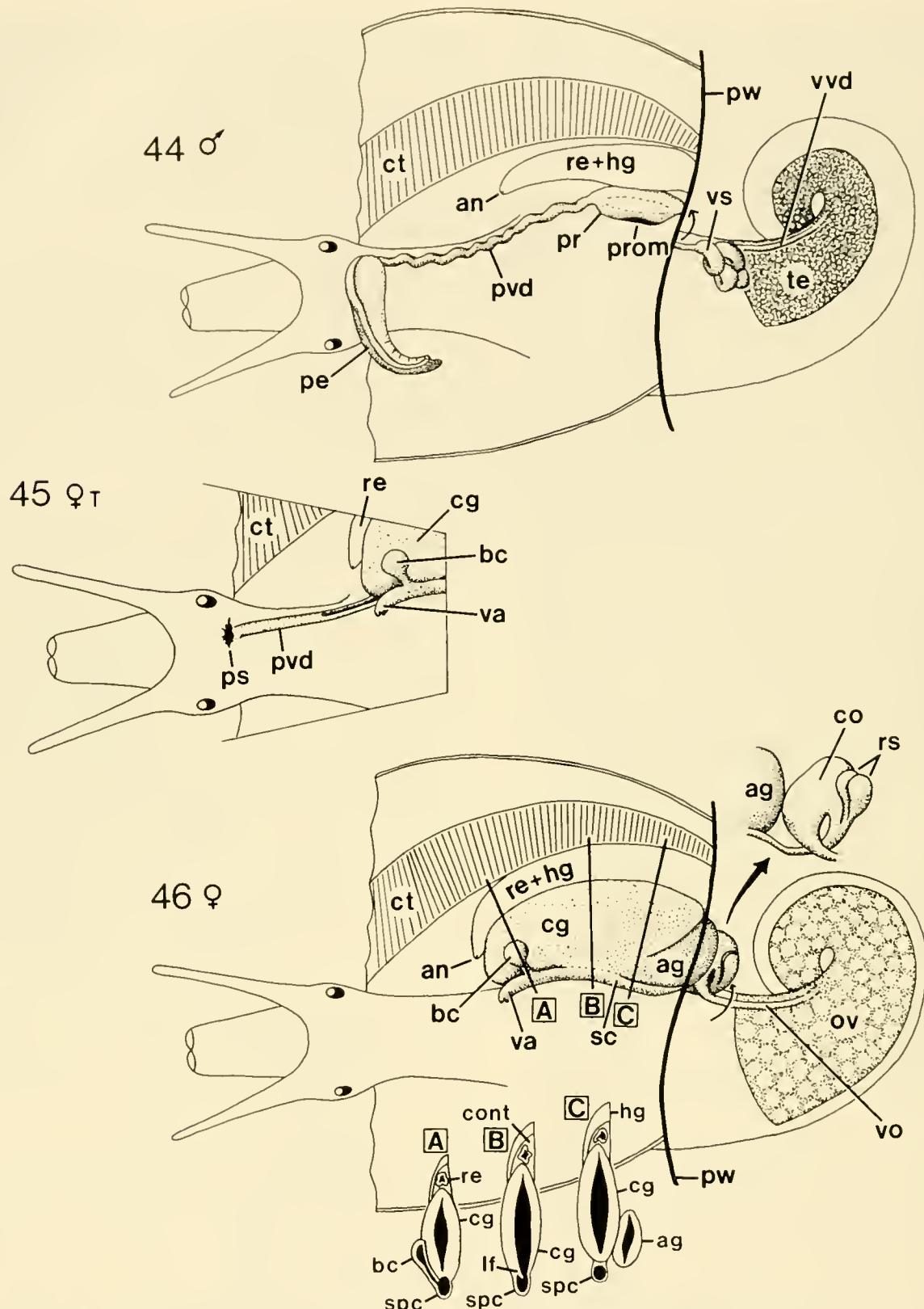
Figures 44–46. *Cyclostremiscus beauii*, reproductive system (semi-diagrammatic). **44.** Male phase. **45.** "Transitional" female phase. **46.** Female phase, with three cross-sections (A, B, C) through female glands. Small arrows indicate reflected organs.

ag, albumen gland; an, anus; bc, bursa copulatrix; cg, capsule gland; co, coiled oviduct; cont, connective tissue; ct, ctenidium; hg, hypobranchial gland; lf, lateral fold; ov, ovary; pe, penis; pr, prostate gland; prom, opening of prostate gland into mantle cavity;

Mating and larval development unknown. Protoconch morphology suggests planktonic veliger stage (see Discussion). Sex change within single individual not observed.

Habits and habitat: To our knowledge, this is the first record of habitat type for this species, *i.e.*, within the burrows of the stomatopod *Lysiosquilla scabricauda*; other published records (see synonymy) refer only to empty shells. Wells *et al.* (1961) recorded *Cyclostremiscus beauii* from the stomachs of *Astropecten articulatus* (Say, 1825), however it is unclear whether the material was alive when swallowed by the starfish. Another specimen from gut contents of *A. articulatus*, in the UNC-IMS collections, from 24 m depth off North Carolina, contained dried animal tissue and is the only other verified live-collected specimen known to the authors. Although burrows of other local species, *e.g.*, callianassid shrimps, polychaetes, hemichordates, and sipunculans, were also sampled, these vitrinellids were not collected in association with any burrower but *Lysiosquilla* during this study.

The snails probably feed on algae, bacterial films and detritus in the burrows. They are capable of handling larger items in their alimentary tract, as evidenced by various shell pieces and foraminiferan shells found in the stomach. From the absence of glandular esophageal pouches and the presence of a crystalline style in the stomach, it can be inferred (Yonge, 1930) that free proteolytic enzymes, capable of digesting animal matter, are not present in this species and would not be expected in this group.

Individuals were almost invariably collected in groups of more than one animal per burrow sample; the maximum number encountered in one burrow sample was seven. *Cyclostremiscus beauii* was twice found crawling openly on sand or seagrass in the vicinity of *Lysiosquilla* burrow openings. In captivity, the animals were active crawlers and were not distracted by light; dark, sheltered areas in the tank (provided by black plastic film containers) were not preferred. During resting periods, all specimens attached themselves to the wall of their container, just above the water level, by means of highly viscous mucus produced by the anterior pedal gland. This behavior was not correlated with food availability or water quality. It might reflect tidal rhythm, but material was not sufficient to test that hypothesis.

Geographical distribution: Western Atlantic, from North Carolina to Brazil (Ceará and Alagoas; *teste* Rios, 1985:41). Recorded from the Pliocene of Jamaica and Florida (see synonymy).

Taxonomic remarks: Fischer (1857b:286), in the original description of *Adeorbis beauii* (in his earlier publication, the name occurred only as a nude list name;

1857a:173), did not give an indication of the number of specimens in the original lot. Moore (1964:132) mentioned a "holotype" in the Paris Museum. However, the single *A. beauii*-specimen in that type collection (MNHN unnumbered, *vidi*) is much smaller than the dimensions given by Fischer (teleoconch diameter 6.3 mm, height 3.5 mm, protoconch diameter 0.42 mm, umbilical diameter 1.1 mm; protoconch whorls 2, teleoconch whorls 2¾; *vs.* 10.5 mm maximum shell diameter in the original description). The specimen is therefore considered the only remaining syntype of a formerly larger lot, and is here selected as lectotype.

Woodring (1928:440) pointed out the close resemblance between Guppy's (1866) *Cyclostrema bicarinata* and *Adeorbis beauii* Fischer, but separated the two because the latter "has a more strongly sculptured base." Smith (1937:67) in turn separated his new species *Circulus stirophorus* from both "*Circulus bicarinatus* Guppy" and "*Circulus beauii* Fischer," by differing numbers of upper and basal spiral ribs. A re-examination of the neotype (Woodring, 1928) of *Cyclostrema bicarinata* (USNM 115621) and the original description and figure of *Circulus stirophorus* Smith revealed that both fall within the range of variation (partly caused by ontogenetic change of basal sculpture) displayed by the Ft. Pierce population, and both are here synonymized (see also Moore, 1964:131). The holotype of *Circulus stirophorus* could not be located. Although the original author indicated the type to be in the MCZ collection, it was never received by that institution (K. J. Boss, personal communication); it was also not located at the Florida State Museum, Gainesville (F. G. Thompson, personal communication).

Cyclostremiscus beauii is the largest vitrinellid in the western Atlantic. Two Recent Panamic species are very similar in size, shape and sculpture:

Cyclostremiscus major Olsson & Smith (1951:46, pl. 3, figs. 1a,b) from Panama differs from *Cy. beauii* in having more numerous spiral ribs throughout and a more rounded periphery (holotype ANSP 187199; figured by Olsson & Smith, 1951).

Cyclostrema gordana Hertlein & Strong (1951:110, pl. 9, figs. 3, 4, 7; holotype CAS 064803, *vidi*) from the Gulf of California, differs conchologically from *Cyclostremiscus beauii* in having a prominent double spiral rib on the base between the basal keel and the umbilicus (see Pilsbry, 1953: pl. 55). Hertlein and Strong (1951: 110) gave the following measurements for the "unique type": maximum diameter 9.7 mm, minimum diameter 7.0 mm, and height 3.3 mm; our examination of the holotype yielded, respectively, 8.6, 6.8, and 3.9 mm. Hertlein and Strong (1951:110) compared *C. gordana* to "*Cyclostrema angulata* A. Adams [1850] from the West Indies" [following "Pilsbry" (= error for Tryon), 1888:

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ps, penis scar; pvd, pallial vas deferens; pw, posterior pallial wall; re, rectum; rs, receptaculum seminis; sc, sperm channel; spc, sperm channel; te, testis; va, vagina; vo, visceral oviduct; vs, part of visceral vas deferens serving as vesicula seminalis; vvd, visceral vas deferens.
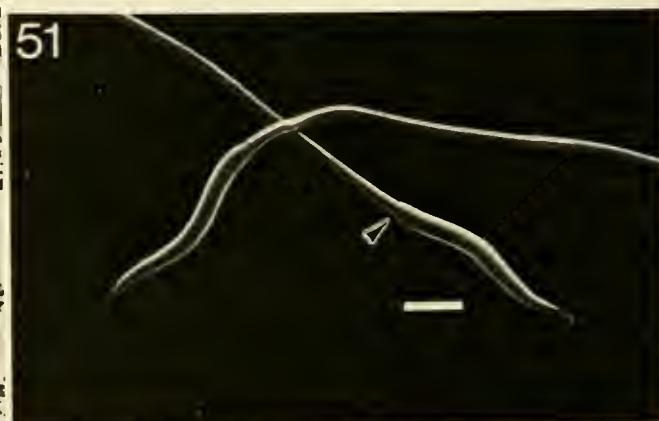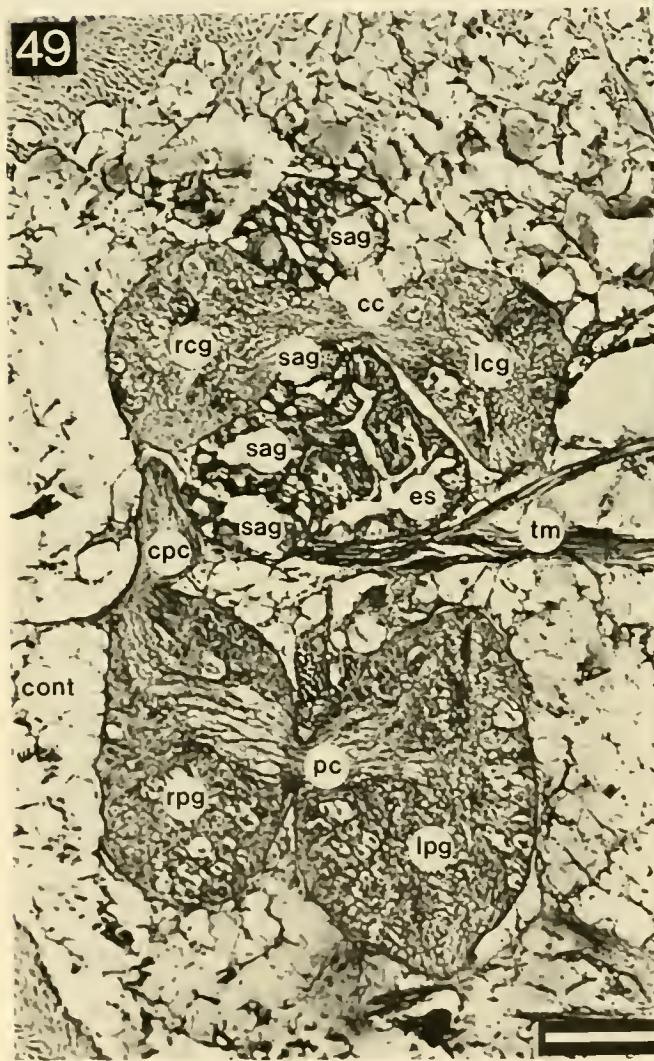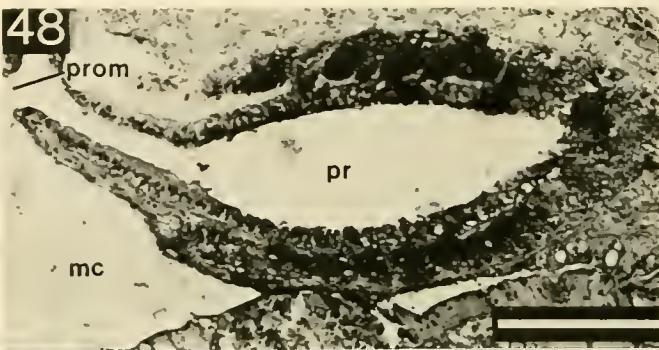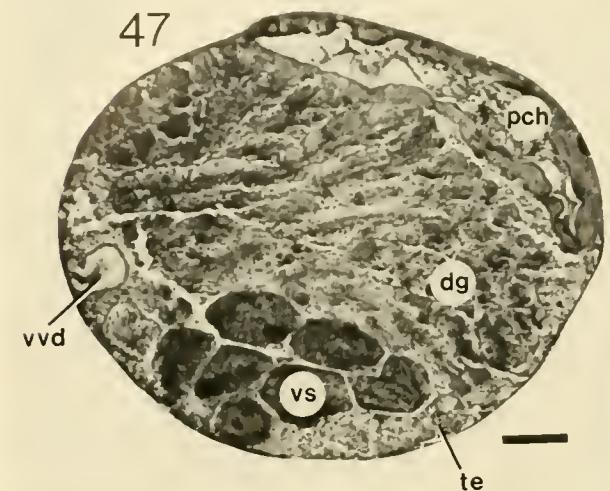
Figures 47–52. *Cyclostremiscus beauii*, specimens from Ft. Pierce Inlet, Florida (light micrographs or critical-point dried SEM preparations). 47. Cross-section through visceral mass (male), at level of vesicula seminalis. 48. Section through prostate, showing
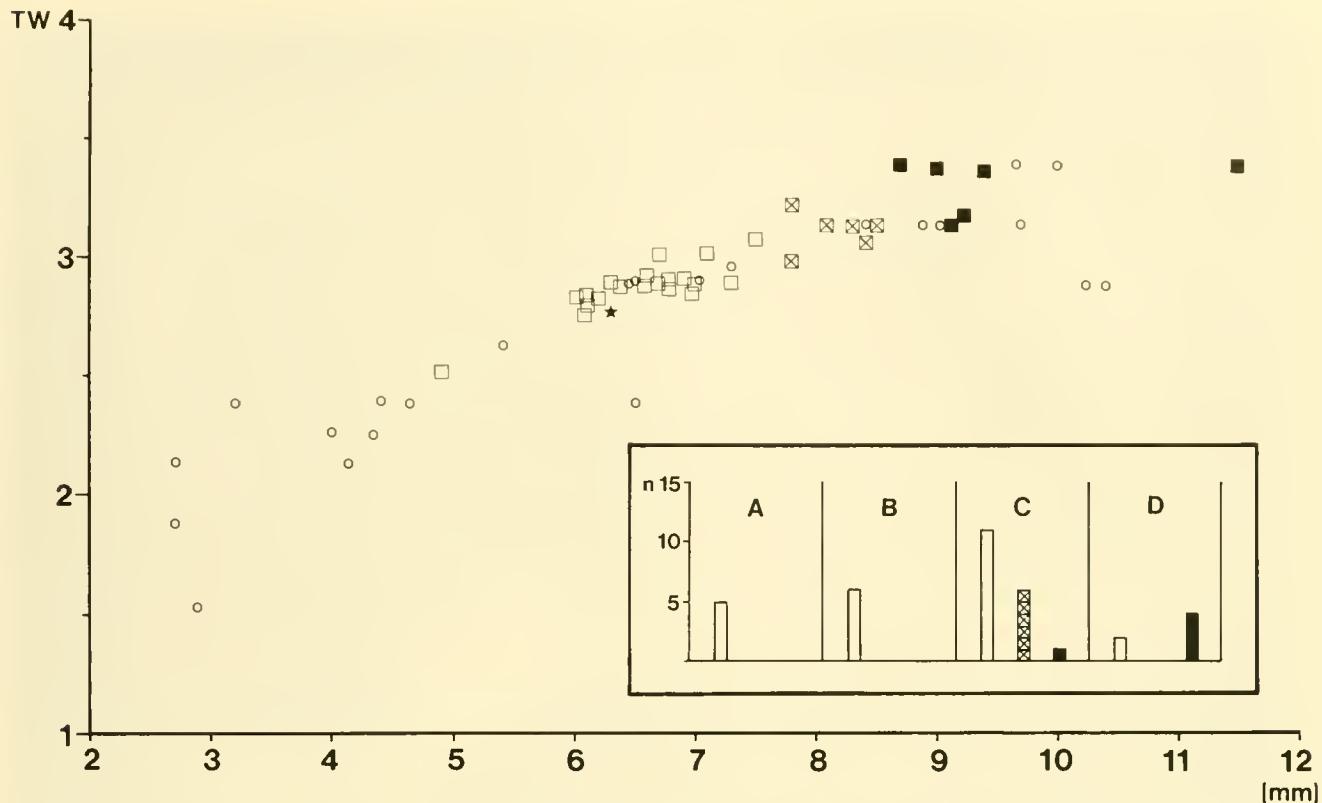
Figure 53. *Cyclostremiscus beauii.* Plot of maximum shell diameter *vs.* number of teleoconch whorls (TW). Inset: Histogram summarizing sex distribution of collections, Ft. Pierce Inlet population. A = collecting period March–July, B = August 1–15, C = August 16–31, D = September, 1987. Open circles = empty shells and unsexed specimens. Open squares = functional males. Cross-hatched open squares = "transitional" females with pallial vas deferens and/or penis scar. Solid squares = females without male structures. Star indicates lectotype specimen (MNHN unnumbered).

92, they considered *C. angulata* a senior synonym of *Cyclostremiscus beauii*—see below] and stated that it differed "principally in the smaller size and more depressed form." However, a re-examination of the *C. gordana* type showed it to differ principally by a strong, second basal keel surrounding the umbilicus. It definitely belongs in the genus *Cyclostremiscus*, as advocated by Keen (1971).

Tryon (1888), followed by Hertlein and Strong (1951), considered *Cyclostremiscus beauii* a synonym of *Cyclostrema angulata* A. Adams, 1850: "*C. angulata*, A. Ad. was described as from the Philippines on the authority of Cuming, but as that great collector sometimes made mistakes, the locality needs confirmation. There can be no doubt of the identity with this species of *C.*

Beaui, Fischer (fig. 63), a West Indian species" (Tryon, 1888:92–93). Tryon's figures (1888: pl. 32, figs. 64, 65) may represent *Cyclostremiscus beauii*. However, as similar species are known from the Indo-Pacific, we feel that the two nominal species should not be synonymized without a re-examination of *Cyclostrema angulata* type material, which could not be located in the British Museum (Natural History) (London) nor in the Redpath Museum (Montreal).

The type species of *Cyclostremiscus*, *Vitrinella panamensis* C. B. Adams, 1852, and several other, similar species (see, *e.g.*, Pilsbry & Olsson, 1945) have distinct axial sculpture which is lacking in *Cy. beauii*, *Cy. major*, *Cy. gordana*, and a number of other nominal species. Pilsbry (1953) described the subgenus *Ponocyclus* in *Cy-*

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lumen and opening into mantle cavity. **49.** Section through circumesophageal nerve ring, with salivary glands. **50.** Spermatozoon (SEM). Arrow indicates junction of midpiece and tail. **51.** Same, detail of two heads (SEM). Arrow indicates junction between head and midpiece. **52.** Cross-section through vagina (left) and rectum (right). Scale bars: 47–49, 52 = 0.1 mm; 50 = 4 μm; 51 = 2 μm.

cc, cerebral commissure; cont, connective tissue; cpc, cerebropedal connective; dg, digestive gland; es, esophagus; hg, hypobranchial gland; lcg, left cerebral ganglion; lpg, left pedal ganglion; mc, mantle cavity; mw, mantle wall; pc, pedal commissure; pch, posterior chamber of stomach; pr, prostate gland; prom, opening of prostate gland into mantle cavity; rcg, right cerebral ganglion; re, rectum; rpg, right pedal ganglion; sag, salivary gland; te, testis; tm, transverse muscle band; va, vagina; vs, part of visceral vas deferens serving as vesicula seminalis; vvd, visceral vas deferens.
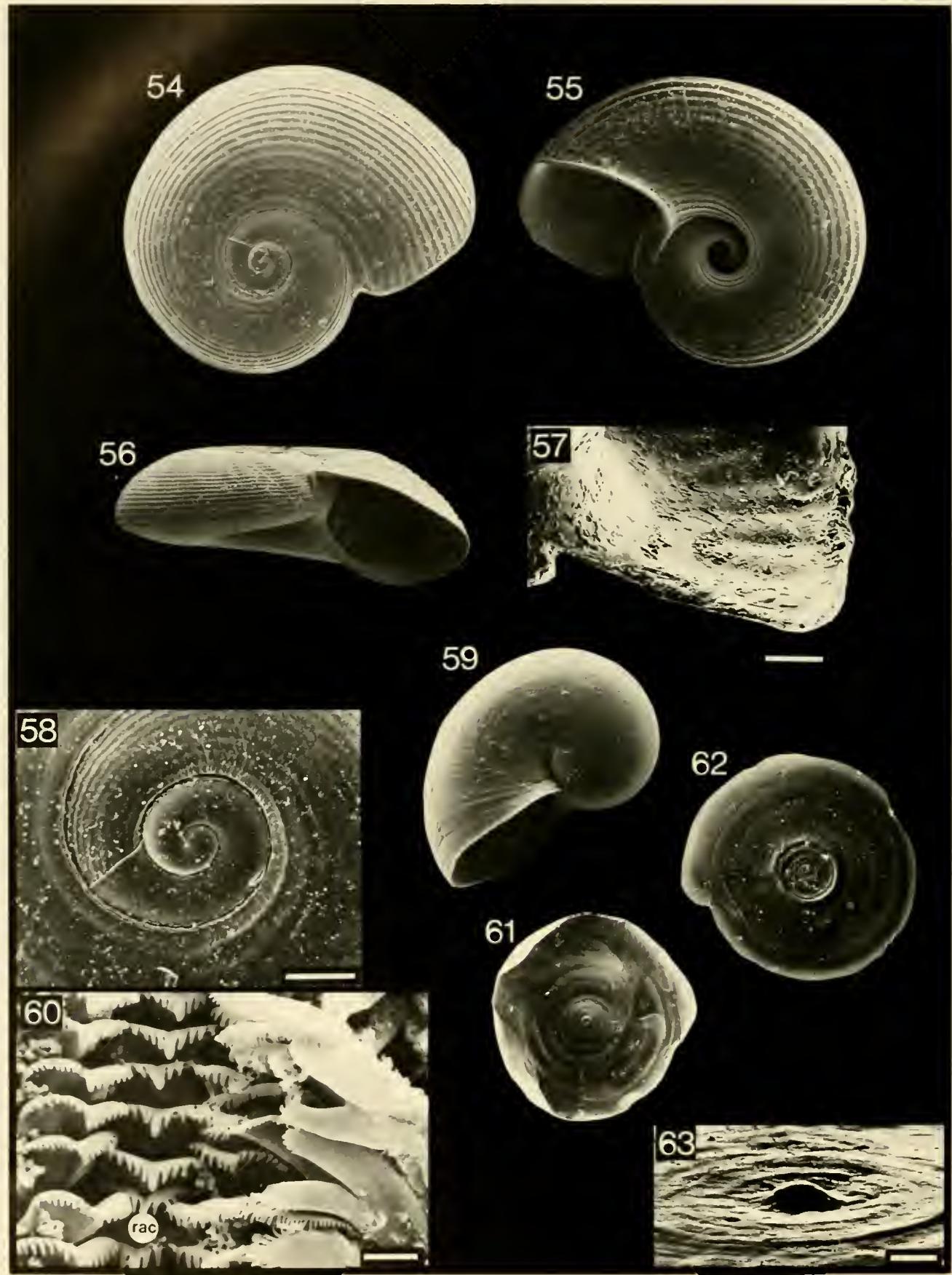
clostremiscus with *Adeorbis beauii* as the type species, and distinguished it from *Cyclostremiscus* by its lack of axial sculpture. As Pilsbry already pointed out in his description of *Ponocyclus* (1953:426), there are a number of species showing intermediate conditions ("weak traces of axial sculpture") and the name is not used here.

Due to the small number of species studied in the Vitrinellidae, little can be said about anatomical characters on the generic level. Aside from the large and elaborately-sculptured shell, the extensive ciliation of the head-foot, and the paddle-shaped pallial tentacle, *Cyclostremiscus beauii* differs anatomically from *Circulus striatus* (see Fretter, 1956), *Ci. texanus* (see below), and *Cochliolepis parasitica* (see Moore, 1972) in having the pallial portion of the intestine straight and uncoiled.

Circulus Jeffreys, 1865 (page 315)

Type species by monotypy: *Delphinula duminyi* Requien, 1848 (page 64; not "*Trochus duminyi* Requien" as usually cited) [= *Valvata*? *striata* Philippi, 1836; see Jeffreys, 1865:317, where he used the junior synonym *D. duminyi* only to avoid secondary homonymy with *Trochus striatus* Linné, 1767].

Circulus texanus (Moore, 1965) new combination (figures 54–68; tables 1, 2)

Vitrinella texana Moore, 1964:66 [unpublished dissertation].
Vitrinella texana Moore, 1965:76, pl. 7, figs. 4–6 [Gulf of Mexico].
? *Vitrinella texana* "Moore, 1964"—Andrews, 1971:73–74, text-fig.—Andrews, 1977:887 [citing "1965"], text-fig. [poor figure; = *Vitrinella* sp., *teste* Odé, 1987:35].
Vitrinella (*Vitrinella*) *texana*,—Abbott, 1974:83.
Vitridomus texana,—Odé, 1987:37.

Material examined: Holotype: empty shell, 1.8 mm, USNM 636311 (Texas). Other material: 15 specimens. FLORIDA: Ft. Pierce Inlet: 2–3 May 1987, 1 unsexed; 24 June 1987, 14 specimens (4 males, 7 females, 2 unsexed, 1 empty shell).

Description

Teleoconch (figures 54–56): Shell small (1.7–1.8 mm diameter, 0.55–0.65 mm height), with 1½–1⅜ teleoconch whorls; almost planispiral, sculptured dorsally and ventrally with about 18 fine spiral ribs; transparent when alive, opaque after death. Ribs slightly stronger, more widely spaced just below suture on dorsum and at periphery, where about 3 ribs form rounded keel below lateral midline. Suture impressed. Ventral surface below keel less convex, often with 30–40 widely-spaced, low axial ribs which are primarily evident from inside of body whorl (figure 57). Umbilicus wide ($\approx 25\%$ of width). Outer lip very slightly reflected; some specimens with one former varix. Aperture at oblique angle to dorsoventral axis. Sutural sinus shallow. Periostracum thin, transparent, with spiral grooves more numerous than on shell surface.

Protoconch (figure 58): Smooth, 0.5 mm diameter, about 2 whorls. No sculptural demarcation separating protoconch I and protoconch II.

External anatomy and organs of the mantle cavity (figures 64–66): Living animal translucent white with buccal mass (visible through proboscis) and protrusible portion of ctenidium rose-pink; digestive gland orange; nerve ring area opaque yellow, visible through integument between eyes. Head with long, extensible snout, rounded and terminally notched at mouth. Ventral side of snout ciliated behind mouth opening, with cilia beating toward mouth. Two long cephalic tentacles with immobile bristles on slightly enlarged tip; motile cilia at least at tip and along side facing snout. Left cephalic tentacle fitting into shallow notch formed by shell keel (figure 65). Eyes black, on slight bulges at base of cephalic tentacles. Neck region very long, slender. Foot elongate, flattened, with anterolaterally recurved corners; finely ciliated sole broadly rounded posteriorly, extending well beyond shell (figure 65). Transverse crease on sole about ⅕ of total length from anterior edge. Anterior pedal mucous gland (figure 65, amg) opening at slit across entire leading edge; mid-ventral fold evident on posterior quarter of sole, but presence of posterior mucous gland not confirmed. Locomotion by ciliary action. Operculum (figures 61–63) corneous, circular, multispiral (*ca.* 8 whorls), with small central peg and rounded-triangular muscle scar on inner surface. Operculum supported by opercular lobes (figure 65, ol) on dorsal side of foot. Lobes simple, unpigmented, without tentacles. Epipodial tentacles absent.

Two finger-shaped pallial tentacles (figure 64, lpt, upt) arising separately but adjacently from inner mantle edge, at right side of animal. Upper (= most dorsal) tentacle unciliated, with immobile terminal bristles, curling into shallow sutural sinus, directed dorsally during crawling. Lower tentacle bearing motile cilia, directed anterolaterally. Ctenidium (figures 64, 65, ct) with numerous finger-shaped filaments, attached for most of its length to internal surface of mantle; anteriormost filaments darker

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Figures 54–63. *Circulus texanus*, specimens from Ft. Pierce Inlet, Florida (SEM) (figures 54–56, USNM 846324). **54.** Shell, apical view (2.7 mm diameter). **55.** Shell, umbilical view (2.7 mm diameter). **56.** Shell, apertural view (2.2 mm diameter). **57.** Inside surface of base of body whorl, showing shallow radial grooves. **58.** Protoconch. **59.** Larval shell, left lateral view (167 µm max. diameter). **60.** Radula. **61.** Operculum, inner surface (0.7 mm diameter). **62.** Operculum, outer surface (0.8 mm diameter). **63.** Operculum, oblique view of inner surface with opercular peg. Scale bars: 57, 58 = 0.2 mm; 60 = 5 µm; 63 = 50 µm.

rac, rachidian teeth.
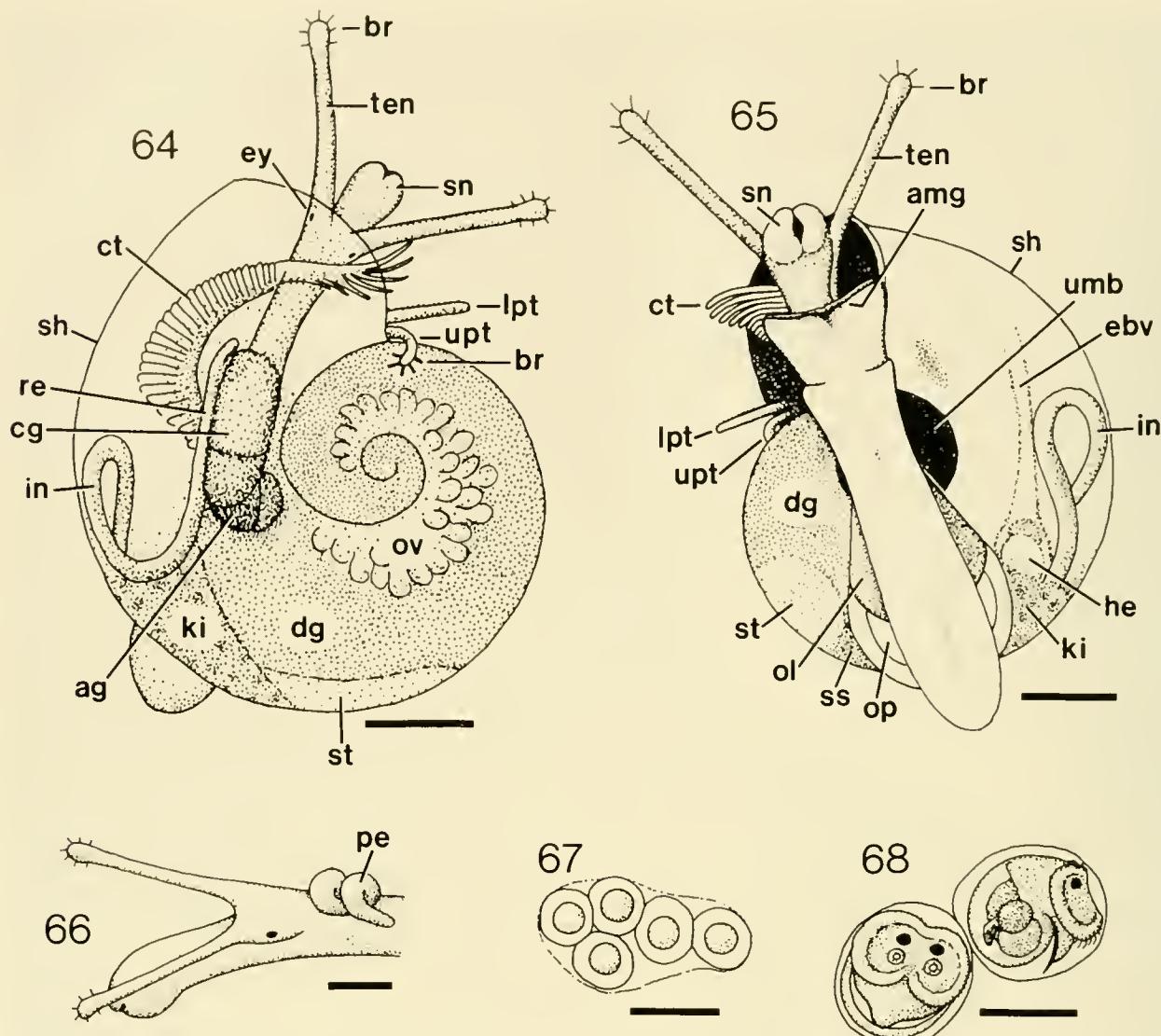
Figures 64–68. *Circulus texanus.* **64.** Crawling female, dorsal view, drawn as with transparent shell. **65.** Crawling animal, ventral view, drawn as with transparent shell. **66.** Head of male, left lateral view, showing penis. **67.** Egg mass. **68.** Two egg capsules, each with veliger larva shortly before hatching. Scale bars: 64, 65 = 0.5 mm; 66, 67 = 0.25 mm.

ag, albumen gland; amg, anterior mucous gland; br, immobile bristles; cg, capsule gland; ct, ctenidium; dg, digestive gland; ebv, efferent branchial vessel; ey, eye; he, heart; in, intestine; ki, kidney; lpt, lower pallial tentacle; ol, opercular lobe; op, operculum; ov, ovary; pe, penis; re, rectum; sh, shell; sn, snout; ss, style sac; st, stomach; ten, cephalic tentacle; umb, umbilicus; upt, upper pallial tentacle.

in color, not attached to mantle skirt, extending out of aperture at right side of head. Extent of osphradium not ascertained.

Alimentary system: Radula (figure 60) taenioglossate. Rachidian tooth wider than long, with acute posterior corners projecting laterally and concave front. Main cusp narrow, unserrated, with 5–6 slightly smaller flanking cusps on each side (number of flanking cusps varying within single radular ribbon) decreasing laterally in size; base with 1 weak elevation per side (in position of basal denticle), midway between posterior corners and central ridge. Lateral tooth with asymmetrical cutting edge, strongly indented at front edge, with narrow, unserrated

main cusp and subequal flanking cusps (6–7 inner, 9 outer). Apex of inner marginal tooth with numerous long, thin, flanking cusps on either side of similarly-sized main cusp. Apex of outer marginal tooth with long, thin inner flanking cusps, slightly more robust than those of inner marginal tooth; cusps at terminus subequal in size; outer margin with 2–3 cusps decreasing in size, remainder of outer margin smoothly rounded. Jaws composed of elements approximately 4 μm in length.

Stomach transparent, with rotating style often clearly visible through shell. Posterior part of stomach not markedly elongated. Intestine (figures 64, 65, in) forming wide loop in posterior part of mantle cavity. Anus just above anterior end of capsule gland in females. Fecal material

as continuous rods of irregular length, rather than pellets, with no obvious surface sculpture.

Reproductive system: Penis (figure 66, pe) a posteriorly directed, counterclockwise, double coil; base arising posterior to eyes, somewhat right of dorsal midline. Testis orange.

Ovary (figure 64, ov) filling inner side of early whorls with grape-like lobes, lighter in color than digestive gland. Capsule gland and much darker-staining (in methylene blue) albumen gland (figure 64, cg, ag) forming compact mass on right wall of mantle cavity, below rectum, terminating anteriorly at level of anus. Position and number of sperm pouches not ascertained.

No evidence of sexual dimorphism associated with possible sequential hermaphroditism. Males both considerably smaller (1.7 mm diameter at 1⅜ whorls) or larger (1.8 mm diameter at 1½ whorls) than females in same sample (1.74–1.78 mm at 1⅜ whorls). One copulation briefly observed, wherein male paused while crawling over dorsal surface of female, with heads adjacent (male at left) and at angle of about 30°. Position of penis not ascertained.

Eggs and larval development: Three weeks after collecting, 7 females and 4 males were placed into glass bowl with seawater (24 °C). Overnight, 15 egg masses were laid; each mass contained 1–5 eggs, each in clear, flattened, circular capsule (egg diameter 110 μm; capsule diameter 170 μm; n = 20). All eggs found in same developmental stage, uncleaved, completely round, finely granular. Soft capsule walls of eggs laid in groups touching each other; each "mass," even if consisting of single egg, coated by sticky, clear, gelatinous layer (figure 67). Eighteen additional egg masses were found in glass jar in which specimens had been kept since collecting. Total number of masses (with respective numbers of single-egg-capsules) was: 4 masses with 1 capsule, 4 masses with 2, 13 masses with 3, 9 masses with 4, and 3 masses with 5 capsules.

One mass with 5 eggs followed through development: From beginning of equal, holoblastic 2-celled stage, 60 minutes elapsed to 4-celled stage, 205 minutes to 8-celled stage, 385 minutes to 16-celled stage, respectively. Gastrula-stage discernible after 11 hours; embryos rotating after 17 hours.

Veliger larvae (figure 68) fully developed at 104 hours, intermittently or constantly rotating, with transparent shell, 2 short veliger lobes, black eye spots (not situated on tentacles at this point), statocysts and operculum [much as described for *Caecum glabrum* by Götze (1938:108, text-fig. 33), but with smaller vela]. Periphery of velar lobes bearing long cilia, underlain by row of shorter cilia. Capsule size now approximately 150 × 120 μm, greatest shell diameter 107 μm, longest dimension of veliger with extended vela 133 μm. During entire process, 3 of 5 embryos developed completely synchronously; other 2 initially about 45 minutes, later several hours, behind. First veligers hatched after 130 hours and swam actively. For following 36 hours, veligers observed either swimming or resting on bottom of bowl, with strong ciliary action on extended vela. No further development noted. Added cultures of mixed single-celled green algae apparently not excepted; all larvae died within next 2 days. [From the size difference between these larvae (170 μm) and the protoconchs of adult shells (500 μm), a longer larval stage, with extensive food intake can be predicted.]

Habits and habitat: Habitat as described for *Cyclostremiscus beauii*. In the laboratory, animals of *Circulus texanus* were very active and fed on normally-occurring algal and bacterial surface films.

Geographical distribution: *Circulus texanus* (type locality: Mustang Island, near Port Aransas) was previously reported to be endemic to the northwestern Gulf of Mexico, and has never been reported alive (Moore, 1964:41; Andrews, 1977:87; Odé, 1987:37). No fossil records are known.

Taxonomic remarks: Moore (1965:77) placed this species in the genus *Vitrinella* C. B. Adams, 1850, and pointed out the differences in shell shape and sculpture in comparison to other species. However, members of *Vitrinella* (based on the type species *V. helicoidea* C. B. Adams, 1850; see tables 1, 2) are generally smooth-shelled or weakly sculptured and are usually furnished with a carina bordering the umbilicus (*e.g.*, Keen, 1971:377; Abbott, 1974:82). We feel that this species is better placed in *Circulus sensu lato* because it agrees in shell shape and sculpture with the type species, *Circulus striatus* from the eastern Atlantic. Odé's (1987:37) placement of this species in *Vitridomus* Pilsbry & Olsson, 1945, cannot be accepted: members of *Vitridomus* [a "rather feebly defined genus" (Pilsbry & Olsson, 1952:36), very similar to *Teinostoma* H. & A. Adams, 1853] have the umbilicus partly covered by a callus.

DISCUSSION

Comparison of the anatomical information on *Cyclostremiscus beauii* and *Circulus texanus* with literature data revealed that published information is scarce or misleading, and that genus- as well as family-level taxa of marine near-planispiral Rissoacea are poorly defined. Three nominal families, Vitrinellidae Bush, 1897, Tornidae Sacco, 1896, and Circulidae (for authorship, see below), are currently in use for members of this group, and the lack of comparative data led Ponder (in press) to treat all three families as a single group in a phylogenetic analysis of the Rissoacea. In the following discussion, we (a) review the available data on species of this complex, (b) compare *Cy. beauii* and *Ci. texanus* with these data and with other members of the Rissoacea, (c) suggest a preliminary grouping for the species for which anatomical data are available, (d) demonstrate the differences between Vitrinellidae and Tornidae, (e) evaluate the taxonomic status of the nominal family Circulidae, and (f) discuss some unusual aspects of the anatomy and reproductive biology of *Cy. beauii*, namely ciliation,

tentacle shape, stomach morphology, and hermaphroditism.

(a) Available literature data (see tables 1, 2).

Except for Fretter's (1956) study of *Circulus striatus*, and Woodward's (1898) and Graham's (1982) work on *Tornus subcarinatus*, most of the available data on the anatomy of marine near-planispiral Rissoacea are restricted to descriptions or illustrations of external morphology, especially Pilsbry and McGinty's (1945a, 1946b) sketches of western Atlantic forms. Some of the few published observations on the radular structure and gross morphology of vitrinellid softbodies are misleading (see also Moore, 1964, 1972). Based on the misconception that these species are archaeogastropods, Bush (1897:127, 142, pl. 22, figs. 12a–g) erroneously constructed a rhipidoglossate radula for *Circulus trilix* (Bush, 1885) [= *Cyclostremiscus pentagonus* (Gabb, 1837), *fide* Moore, 1964: 138]. The "supplementary plicated gill" (Stimpson, 1858: 308) of *Cochliolepis parasitica* was not found in that species by Moore (1972:101). Pilsbry (1953:427) mentioned a taenioglossate radula for *Cyclostremiscus beauii*, and added "This will be figured in a paper now in preparation by T.L. McGinty and the author." This work was apparently never published.

(b) Comparison of *Cyclostremiscus beauii* and *Circulus texanus* with other vitrinellids and rissoaceans.

Both *Cyclostremiscus beauii* and *Circulus texanus* display "typical" rissoacean characters (as outlined by Fretter & Graham, 1978:153; Boss, 1982:984; Ponder, 1983, in press) and agree to a large extent with the previous concept of Vitrinellidae (Fretter, 1956; Moore, 1972; see tables 1, 2, Group 1). As in most other vitrinellid species, the cephalic and pallial tentacles bear immobile bristles and/or motile cilia. Tracts of motile cilia on the cephalic tentacles occur in numerous groups in the Rissoacea; for lack of comparative data, it is not yet clear whether the arrangement of these cilia in grooves, as in *Cy. beauii*, is unusual. Photographs of critical-point dried tentacles of a freshwater rissoacean, the hydrobiid *Tryonia clathrata* Stimpson, 1865 (see Hershler & Thompson, 1987: 27, figs. 13–17), show no grooves present in that species.

Cyclostremiscus beauii and *Circulus texanus* have two closely-spaced pallial tentacles on the right side. This arrangement is present in most studied vitrinellids (the exception being *Cochliolepis albiceratus* Ponder, 1966), in the type species of *Tornus* (Tornidae, see below), in *Hydrococcus brazieri* (T. Woods, 1876) (monotypic Hydrococcidae, see Ponder, 1982), and in the rissoid genus *Rissoina* Orbigny, 1840, where some species have either the anterior (right) or posterior (left) pallial tentacle bilobed (Ponder, 1985:78). As described for *Cy. beauii*, the function of the upper tentacle, which usually bears immobile bristles, and is held upright and bent around the aperture, is clearly sensory, while the lower one, often distinctly ciliated and sometimes broadened, controls and/or enhances water flow.

Both species have a small central opercular peg which is probably not homologous with the lateral "neritid-type" peg in other families of Rissoacea (character considered plesiomorphic in this superfamily), while the circular shape of the vitrinellid operculum is considered derived (Ponder, 1985:5).

The osphradium of *Cyclostremiscus beauii* is very similar to those described for *Circulus striatus* (see Fretter, 1956:372) and for species of the Rissoidae (Johansson, 1939:319, pl. 3, figs. 3, 4, text-fig. 5; Haszprunar, 1985: 476, figs. 7k, 16).

The radulae of the two species studied here have only one pair of basal denticles (or elevations) on the rachidian tooth, a feature known from some other rissoacean families, such as Hydrobiidae (see Bandel, 1984:29, text-fig. 47) and Rissoidae (see Ponder, 1985:10). This character was hypothesized to be primitive in the Rissoacea by Ponder (1985:119).

The position of the salivary glands relative to the circumesophageal nerve ring is often used in family- and superfamily-level discussions (*e.g.*, Ponder, 1983:236, 258; in press). However, as a highly variable character in the populations of *Cyclostremiscus beauii* studied herein, further data on additional species are necessary before it can be reliably utilized to infer phylogenetic relationships of the Vitrinellidae.

The extensive anterior section of the esophagus of *Cyclostremiscus beauii*, with its long, coiled, dorsal folds, is very similar to that of *Hydrococcus brazieri* (see Ponder, 1982:77).

The conspicuous ciliated tract leading from the renal opening to the head of *Circulus striatus* (see Fretter, 1956:372) is lacking in *Cyclostremiscus beauii*.

The presence of markedly vacuoled connective tissue in *Cyclostremiscus beauii* is a character shared by *Circulus striatus* and *Tornus subcarinatus* (see Graham, 1982:147).

The nervous system of vitrinellid species is typically rissoacean and shows moderate (*Cyclostremiscus beauii*) to high (*Circulus striatus*; Fretter, 1956:377) concentration. The RPG ratio of *Cy. beauii*, averaging 0.49, lies within the range of those of members of the rissoacean family Pomatiopsidae (see, *e.g.*, Davis & Mazurkiewicz, 1985:45, table 8).

The structure of the male and female reproductive systems encountered during this study is rissoacean (*e.g.*, Johansson, 1956). As in most other rissoaceans (*e.g.*, Ponder, 1985:6), the albumen and capsule glands form a single, continuous mass [a character not recognizable from Fretter's (1956) description and figures of *Circulus striatus*]. The Vitrinellidae differ from the Rissoidae (*e.g.*, Ponder, 1985: text-fig. 2) wherein a non-homologous structure, an expanded part of the upper oviduct, posterior to the bursa copulatrix and/or receptacula seminis, functions as an albumen gland. This "upper oviduct gland" of the Rissoidae is homologous with the coiled part of the visceral oviducts of the Hydrobiidae (see Johansson, 1956) and Vitrinellidae [Fretter's (1956) "renal oviduct"].

Most members of the Rissoacea have one bursa copulatrix and one receptaculum seminis near the posterior

pallial wall, requiring the sperm to travel the entire length of the sperm channel (vaginal lumen, sperm groove of the ventral channel of authors) immediately after copulation. Others have developed additional, distal sperm pouches (anterior sperm-storage structure, distal blind sac, sac-like vestibule, spermatheca, pseudo-bursa of authors), either in addition to [e.g., *Pusillina inconspicua* (Alder, 1844); see Johansson, 1939:337, text-fig. 22 (as *Rissoa*); Rissoidae], or instead of the proximal bursa copulatrix [e.g., *Hyala vitrea* (Montagu, 1803); see Johansson, 1949: text-fig. 1; Iravadiidae]. These distal sperm pouches are not necessarily homologous with each other and certainly not with the proximal bursa (see, e.g., Slavoshevskaya, 1978). Vitrinellids for which such data are available (*Circulus striatus* and *Cyclostremiscus beauii*) differ from most other rissoaceans in the presence of two more-or-less equally developed, proximal receptacula seminis which, in position and size, look much like the two sperm sacs (i.e., bursa copulatrix and receptaculum seminis) of other Rissoacea (e.g., in the rissoid *Lucidestea* Laseron, 1956; see Ponder, 1985:67, text-fig. 3). Whether the presence of two proximal receptacula seminis is a distinguishing character for Vitrinellidae cannot yet be determined, as accessory receptacula have been demonstrated for members of the genus *Alvania* in the Rissoidae (Johansson, 1956; Ponder, 1985). In both *Circulus striatus* (see Fretter, 1956:377) and *Cyclostremiscus beauii*, the distal end of the coiled oviduct serves as the fertilization area, and not as an additional functional receptaculum as has been reported for some other rissoaceans [e.g., *Alvania subsoluta* (Aradas, 1847), where the distal end contained oriented sperm; Johansson, 1956: 380].

The spawn mass of members of the Rissoidae usually has numerous eggs per capsule in planktonic forms, while one-egg-per-capsule is characteristic of "direct" development (see Lebour, 1937; Thorson, 1946). This does not hold true for the spawn of *Circulus texanus*, which generally resembles that of the freshwater rissoacean *Bithynia tentaculata* (Linné, 1758), as described and illustrated by Ankel (1936:164, text-fig. 142B). [The number of eggs there, however, is larger (4–24; Lilly, 1953:104), and hatching occurs at the crawling stage]. Jablonski and Lutz (1980:336; after Taylor, 1975) stated that the Rissoacea ". . . follow one of two developmental pathways: those that hatch as crawling juveniles from relatively large eggs (140–320 μm) and those that hatch from relatively small eggs (60–130 μm) and spend 2–3 weeks as planktonic veligers." Both species studied here definitely fall into the latter category: veliger shells of *Circulus texanus* (figure 59) were one full whorl smaller than the final larval shells as seen in the adult protoconch (figure 58); the protoconch of *Cyclostremiscus beauii* (figures 9–11) shows a distinct line and change of sculpture between protoconch I and protoconch II, with almost another full whorl of growth before metamorphosis, suggesting several weeks (K. Bandel, personal communication) of planktonic life. In his unpublished revision of western Atlantic Vitrinellidae, Moore (1964:18) inferred that

"most, if not all, species appear to have a planktonic veliger stage of some duration."

The sperm cells of *Cyclostremiscus beauii* are of the general type known for other members of Rissoacea (see Götze, 1938; Franzén, 1955). The twisted acrosome and relative lengths of head, midpiece and tail are similar to those described by Franzén (1955) for *Caecum glabrum* (Montagu, 1803). The head is much shorter than that of the two rissoids previously studied [*Pusillina inconspicua* (Alder, 1844) (as *Rissoa*) and *Onoba striata* (J. Adams, 1797); Franzén, 1955:406–409], and the relative length of the midpiece much greater than in *Hydrobia ulvae* (Pennant, 1777).

Direct communication of the coiled ("renal") oviduct with the kidney (Fretter, 1956), previously considered unique for *Circulus* or the Vitrinellidae, is now also known for other families of the Rissoacea (Tornidae, Graham, 1982; Truncatellidae, Fretter & Graham, 1962).

Anatomical characters of *Circulus striatus*, which Fretter (1956:380) discussed as probably "associated with small size and body form," are equally expressed in the much larger *Cyclostremiscus beauii*, suggesting that Fretter's hypothesis was incorrect.

(c) Preliminary grouping of "vitrinellid-like" species for which anatomical data are available.

The species for which sufficient gross morphological data are available appear to fall into three groups, two of which are here considered of familial rank and one comprising species of *incertae sedis* (tables 1, 2). Members of Group 1, currently placed in the genera *Vitrinella*, *Teinostoma*, *Pleuromalaxis*, *Cochliolepis*, *Circulus* and *Cyclostremiscus*, are here considered to belong to the Vitrinellidae (the placement of the species described as *Cochliolepis albicerata* Ponder, 1966, is somewhat doubtful as it has only one pallial tentacle, and the morphologies of its osphradium and penis are unknown). Some of the characters attributed to the family Vitrinellidae in Moore's dissertation (1964) were based on *Parviturboides interruptus* (C. B. Adams, 1850) (tables 1, 2, Group 2), later considered a species of uncertain systematic position (Moore, 1972:107). This species differs from the other forms here grouped in Vitrinellidae by the following anatomical characters: posterior foot margin with immobile cilia, left cephalic tentacle with four low swellings on proximal posterior border, penis with glandular area and directed straight back. Another species, *Tomura bicaudata* (Pilsbry & McGinty, 1946) differs in many head-foot characters (tables 1, 2, Group 2) and is here also considered as *incertae sedis*. White (1942:92) advocated the inclusion of "*Cyclostrema*" *bushi* Dautzenberg & Fischer, 1907, in the Vitrinellidae/Tornidae complex and published anatomical descriptions and illustrations of that species. While some morphological characters [head with well-developed eyes and terminally ciliated cephalic tentacles, the well-developed osphradium (1942: text-fig. 6), and the circular, multispiral operculum (1942: pl. 2, fig. 3)] agree well with the species listed here as vitrinellids, the glandular pouches

in the esophagus and, most of all, the pair of epipodial (not pallial) tentacles on the right side of the animal (White, 1942:90, text-fig. 5), prevent inclusion in Vitrinellidae. *Tornus subcarinatus* (tables 1, 2, Group 3) is here considered a member of a separate family (see below).

(d) Family relationships: Vitrinellidae-Tornidae.

Several attempts have been made to define the key characters of the family Vitrinellidae (*e.g.*, Moore, 1965: 74, 1969:170, 1972:107ff.; Boss, 1982:991). However, because of the small number of species fully studied anatomically, no single synapomorphy defining the family is clear at this time. The most obvious features of the Vitrinellidae are: a low-spired, translucent white shell; long cephalic tentacles equipped with terminal bristles and, in most cases, motile cilia; two closely-spaced pallial tentacles on the right side; a large monopectinate gill often projecting to the right of the head; a large linear osphradium; a foot with simple or only slightly indented anterior and posterior margins; a horny concentric, multispiral operculum; and the possession of a non-glandular curved penis in the male. Some of these features (shell shape, pallial tentacles, and projecting gill) have led authors (*e.g.*, Taylor & Sohl, 1962) to synonymize Vitrinellidae and Tornidae, based on Woodward's (1898) work on *Adeorbis* [= *Tornus*] *subcarinatus* (Montagu, 1903). Others (*e.g.*, Adam & Knudsen, 1969; Moore, 1972) have pointed out differences between vitrinellids and *Tornus*/tornids in features of the eyes (functional eyes are lacking in *T. subcarinatus*) and/or the operculum (oval and paucispiral in *T. subcarinatus*) and have separated the two families. In a redescription of the anatomy of *T. subcarinatus*, Graham (1982:147) saw the opercular shape as the "single difference" between the two nominal families and again advocated synonymy.

Additional anatomical characters of Tornidae that warrant separation from Vitrinellidae are: (1) the conspicuous, elongate osphradium of the latter is not present in *Tornus* (Graham, 1982:144, found only "a small ciliated groove, which may be a reduced osphradium"), (2) the attachment of the ctenidial axis to the mantle is short and the axis hardly supplied with blood vessels, and (3) the penis of *T. subcarinatus* bears several finger-like processes which are not known in vitrinellids as delimited here. [Fretter & Graham (1978:231) described the ctenidium of *T. subcarinatus* as "partly bipectinate." This is apparently in error, as both Woodward (1898) and Graham (1982) described and illustrated that gill with only a single row of lamellae.] As *T. subcarinatus* lives in a comparable habitat (under boulders on well-oxygenated sand or mud) and is of about the same size as *Circulus* spp., the drastic difference in osphradial type indicates phylogenetic difference rather than specialization on a low taxonomic level.

Ponder (in press) combined the "tornid-vitrinellid-circulid complex" as family Tornidae for the purpose of his phylogenetic analysis of the Rissoacea. However, most of the characters and character states he attributed to

that complex (metapodial tentacle present, esophageal pouches and glands present, penial glands present, osphradium short, posterior end of foot not simple) do not occur in Vitrinellidae as understood here, and must refer to *Tornus* and other tornid genera studied by Ponder (*Pseudoliotia* Tate, 1898, *Scrupus* Finlay, 1927; unpublished).

Vitrinellidae and Tornidae fit well into the Rissoacea, and an independent grouping of these families as Tornacea (*e.g.*, Kuroda *et al.*, 1971; Golikov & Starobogatov, 1975) is not justified. The family Adeorbidae Monterosato, 1884, used by some authors for members of this complex, is a synonym of Tornidae, since *Adeorbis* S. Wood, 1842, is an objective synonym of *Tornus* Turton & Kingston, 1830 (see Iredale, 1914:172, 1915:344).

(e) The nominal family Circulidae.

The taxonomic status of the nominal family Circulidae remains problematic. The family name "Circulidae" was first used by Fretter and Graham (1962:642, "Appendix 1"), in a list of taxa treated in that publication. The text reads merely "Circulidae: *Circulus striatus* (Philippi)." Fretter and Graham (1962) did not state that they intended to create a new family, did not mention the name in the main body of the text, even when the taxonomic position of the genus (1962:550, 618) and the composition of the superfamily (1962: 622–623) were discussed, and in fact never used any family name but Vitrinellidae when they referred to *Ci. striatus* in subsequent publications (Fretter & Graham, 1978:227; Graham, 1982: 147). Lacking any description, definition, or bibliographic reference, a name thus introduced is not taxonomically available (ICZN, 1985: Art. 13). "Circulidae" could therefore be regarded as a *nomen nudum*.

However, Golikov and Starobogatov (1975:211) accepted "Circulidae Fretter & Graham, 1962" as a valid family and stated (1975:218) that "the characteristics of the latter family are found in Fretter (1956:381)," thereby referring to the summary of Fretter's description of *Ci. striatus*. This fulfills the requirement of ICZN (1985) Art. 13(a)ii (Bibliographic Reference to Published Statement) and, unless there are earlier such statements that have escaped us, this makes Golikov and Starobogatov (1975) the authors of Circulidae, with *Circulus* as the name-bearing type. The nominal family Circulidae is, with anatomical descriptions available for *Ci. striatus* and *Ci. texanus*, much better defined than the Vitrinellidae, where our knowledge of *Vitrinella* is based only on shell characters and Pilsbry and McGinty's (1945a, 1946b) sketches of crawling animals (tables 1, 2). All available data suggest synonymy of Vitrinellidae and Circulidae (tables 1, 2; Boss, 1982:991). In any case, the placement of Vitrinellidae and Circulidae in separate superfamilies, or even separate superorders (Golikov & Starobogatov, 1975), is highly exaggerated.

(f) Unusual features of *Cyclostremiscus beauii*.

The study of *Cyclostremiscus beauii* revealed a number of features that differ from other members of the Vitrinellidae (and, in part, from the Rissoacea). Most of

these features may be related to either its unusually large size (for a vitrinellid) or its unusual habitat in stomatopod burrows.

Ciliation and tentacle shape: The extensive ciliation of the gills, cephalic tentacles and lower pallial tentacle provides effective respiratory and excretory currents. On the right side of the head, where in- *and* outgoing currents are present, water flow is controlled by the paddle-shaped tentacle. Low tides and high water temperatures are likely to create anoxic conditions in the burrows, and a large vitrinellid such as *Cyclostremiscus beauii* may be more strongly affected by oxygen deficiencies than, for instance, the smaller *Circulus texanus*, and thus would benefit from an elaborate system to produce and direct currents. The only other known commensal vitrinellid, *Cochliolepis parasitica*, is much smaller, and lives directly on its host [under the scales of the giant scale worm *Polyodontes lupina* (Stimpson, 1856); see Stimpson, 1858; Hartman, 1945:10]. Moore (1972:104) did not find cilia on the gill filaments of *Cochliolepis parasitica*, suggesting that currents produced by the annelid are sufficient to supply the snail. All other species studied live under rocks (table 2).

Stomach: The rissoacean stomach does not normally have a caecum or an elongated posterior chamber, as occurs in various other prosobranchs ("it is not possible to see any trace of it in the . . . Rissoacea"; Fretter & Graham, 1962:225). Only a few exceptions are known: Ponder (1985:78) described the stomach of *Rissoina* (Rissoidae) as "very long due to elongation of posterior chamber," and Ponder (in press) listed the character state "posterior gastric chamber not small" for the families Emblandidae, Truncatellidae and Stenothyridae. The presence of a large posterior chamber in *Cyclostremiscus beauii*, similar in relative shape and organization to that of *Pomatias elegans* (Müller, 1774) (Pomatiasidae), as described by Graham (1939:90, fig. 6D), is therefore surprising. It may allow *Cy. beauii* to maintain a regular supply of food particles by regulating fluctuations in the rate of food intake (as suggested by Graham, 1939:93, for *Pomatias*), especially since feeding must be strongly affected by tidal, and therefore water-level, changes within the stomatopod burrows. A relatively large animal such as *Cy. beauii* would be more strongly affected than smaller vitrinellids, *e.g.*, *Circulus texanus*, which were observed to feed in very small pockets of water (personal observation), thus maintaining a more-or-less continuous feeding activity, as has been described, *e.g.*, for a member of the genus *Caecum* (Morton, 1975:14).

Hermaphroditism: The most striking result of this study was the discovery of small functional females in *Cyclostremiscus beauii* with apparently functionless remnants of the male reproductive system. Penial structures are known to occur in various female rissoaceans (particularly hydrobiids and rissoids). Thiriot-Quiévreux (1977:779ff.) based her hypothesis of sequential hermaphroditism in four species of *Rissoa* on the presence of more-or-less developed penes in immature specimens

and females. However, a later in-depth study (Thiriot-Quiévreux, 1982:167ff.) of these species through annual cycles showed a seasonal (and geographical) pattern of penis-size distribution in females, but no evidence of sex change. The survey did "not support the hypothesis of a successive hermaphroditism" (1982:167). In *Cyclostremiscus beauii*, remnants of the male apparatus are only evident in the smallest functional females (figure 53), with a gradual decrease of male structures with size. As outlined above, we take this as evidence for a sex change in this species rather than a simple sexual dimorphism in shell size. During ontogeny, the male reproductive system apparently disappears completely and is replaced by female organs. The anteriormost part of the pinkish-orange female albumen gland is found in the same relative position as the prostate (of similar color and reaction to staining) in the male phase. As no animal was found with a very early stage of development of the albumen gland, it cannot be decided whether these organs, or parts of them, are homologous. [Reid (1986), in a study of *Mainwaringia* Nevill, 1885, the first reported case of protandrous sequential hermaphroditism in the Littorinacea, found both a closed pallial oviduct and an open prostate in the intersexual and female stages, "suggesting that these structures are not strictly homologous" (1986:225). In that littorinid group, small penes are retained in the female phase (1986:237), and the pallial oviduct opens into the also-retained pallial vas deferens, then serving to carry egg capsules (1986:238).] With this admittedly small data set for *Cy. beauii* from only two localities, and the absence of data on individual development and longevity, settlement cues and adult mobility, several scenarios could be constructed. It is, for example, theoretically possible that functional males arrest growth to prolong the male phase, or that the change into the female phase occurs only after successful mating as a male. However, no evidence was found to consider this sex change as labile, *i.e.*, environmentally mediated, as is known for other caenogastropod families such as Calyptraeidae and Stiliferidae (see Hoagland, 1978, for examples and discussion). The data are further insufficient to demonstrate either seasonal or partner-induced change. The sex change in *Cy. beauii* appears to occur only once, at a predetermined size (figure 53; about 8 mm shell diameter, 3 teleoconch whorls), and it apparently affects most, if not all, individuals (as the general shift in gender over time in the Ft. Pierce population suggests).

Thus *Cyclostremiscus beauii* is interpreted as a protandrous sequential hermaphrodite. The term sequential (= consecutive, successive) is important here. In a review of the terms protandry, protogyny and hermaphroditism, Hoagland (1984:86) defined *protandry* as "the functioning of an organism first as male, then as female, with no further sex change. The two sexual phases are separated by a phase in which male primary and secondary sex characters disappear, and the animal re-differentiates as a female." This however omits those species which, after an initial male-only phase, have both male and female

reproductive systems developed and functional (*e.g.*, members of Rissoellidae and Omalogyridae; see below), *i.e.*, protandrous simultaneous hermaphrodites. [Simultaneous hermaphrodites, in our understanding, do not necessarily use "the same gonad to produce both eggs and sperm" as defined by Hoagland (1984:85).]

Although, at this point, we do not know whether protandrous sequential hermaphroditism is the exception, rather than the rule, in this family, the occurrence of hermaphroditism in *Cyclostremiscus beauii* could be interpreted as an adaptation to its peculiar habitat characterized by low density and relative isolation. Protandrous sequential hermaphroditism has an advantage for *Cy. beauii*, as each individual thereby minimizes the age at which it first reproduces and increases the likelihood of finding a compatible mate in a small group. Inbreeding between siblings would also be reduced (see Ghiselin, 1969, for discussion).

Members of the approximately 25 families grouped under Rissoacea are generally described as gonochoristic (see, *e.g.*, Boss, 1982:984), although possibly derived from ancestors that were sequential hermaphrodites (Slavoshevskaya, 1984). Reported cases of hermaphroditism in prosobranchs (*e.g.*, Webber, 1977:10; Fretter, 1984:15) include only two genera that have classically been assigned to this superfamily, *Omalogyra* (Omalogyridae) and *Rissoella* (Rissoellidae). Fretter (1948) described in detail the anatomy and reproductive biology of *O. atomus* (Philippi, 1841) and *R. diaphana* (Alder, 1848). Both species were found to be protandrous simultaneous hermaphrodites, with some likelihood of self-fertilization in *O. atomus* (1948:612, 621, 630; see also Fretter & Graham, 1962:381, and 1978:218, 223). [Fretter & Graham, 1964:134, refer (erroneously?) to the same two species as being "protandrous consecutive hermaphrodites."] Both families have been subsequently removed from the Rissoacea and have been recently placed outside the Caenogastropoda, near (Salvini-Plawen & Haszprunar, 1987) or in (Ponder & Warén, in press) the Allogastropoda (= Heterostropha of authors). Thus, *Cyclostremiscus beauii* is to our knowledge the only species in the superfamily Rissoacea for which protandrous sequential hermaphroditism has been demonstrated. However, as sequential hermaphroditism is not as easily recognized as simultaneous hermaphroditism, it might be more widely distributed in the Vitrinellidae and/or other families of this group. The mismatch in descriptions of the male reproductive system of *Tornus subcarinatus*, where a penis was lacking according to Woodward (1898) and was found by Graham (1982), might find an explanation after all.

ACKNOWLEDGEMENTS

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Geographical Distribution of Some Epitoniidae (Mollusca: Gastropoda) Associated with Fungiid Corals

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ABSTRACT

The known ranges of three coral associated epitoniids, *Epitonium costulatum* (Kiener, 1839), *Epitonium ulu* Pilsbry, 1921, and *Epitonium bullatum* (Sowerby, 1844) are reviewed.

INTRODUCTION

The family Epitoniidae has had a complicated nomenclatural history, with more than 3,000 Recent and fossils species named. The genus *Epitonium* is an overwhelmingly large group about which much has been published, but information on habitats, ecology, growth patterns, and reproduction is known for relatively few species. Some epitoniids are perhaps the only gastropods except certain coralliophilidae to have feeding associations with fungiid corals.

The stony corals comprise a large group of animals showing a great variety of form. Wells (1956:F388) listed 11 living genera in the family Fungiidae Dana, 1846, and further stated, "Within the family Fungiidae some animals are attached as juveniles, but as adults become detached and live free on rubble substrates. Others remain attached throughout their lives." There are 11–12 genera, within which are probably 49 species. Fungiids live in warm seas in water temperatures 22 °–33 °C. The corallum (skeleton) is rounded or elongate, varying in length from about 5 cm to 35 cm, and in width from 5 cm to 20 cm. Known commonly as "hat" or "mushroom" corals, living *Fungia* spp. are pink, green, off-white, or pale tan. Distribution of these corals is extensive, from the east coast of Africa, across the Arabian Sea, the Bay of Bengal, Western Pacific Ocean and including the Southern and Eastern Pacific oceans.

Previous reports of epitoniids associated with *Fungia* are those of Root (1958:8), Robertson (1963:57, 1965:7, 1970:45), Bosch (1965:267), Taylor (1977:254), Kay (1979:152), Bell (1982:508, 1985:161), Sabelli and Taviani (1984:92). These papers report at least three species of epitoniids associated with species of *Fungia*.

A collection of *Epitonium* spp. made by SCUBA divers in the northern Red Sea verified that *Fungia* is "home" to the following species of epitoniids: *Epitonium costulatum* (Kiener, 1839), originally described from an unknown locality; *Epitonium ulu* Pilsbry, 1921, originally described from Hawaii; and *Epitonium bullatum* (Sowerby, 1844), originally described from the Philippines. An unidentified *Epitonium* sp. associated with *Fungia* was also reported by Sabelli and Taviani (1984) from the Red Sea.

The following abbreviations appearing in the text are defined as follows:

ANSP—Academy of Natural Sciences, Philadelphia, PA.
GENEVA—Muséum d'Histoire Naturelle, Geneva, Switzerland.
NHM, L.A.—Natural History Museum, Los Angeles County, Los Angeles, CA.
Bratcher Collection—Twila Bratcher, Los Angeles, CA.
Chaney Collection—Henry Chaney, Redondo Beach, CA.
DuShane Collection—Helen DuShane, Whittier, CA.
Kaiser Collection—Kirstie Kaiser, Park City, UT.

RECORDS

Epitonium costulatum (Kiener, 1839)
(figures 1, 2)

Discussion: *Epitonium costulatum* (Kiener, 1839) as far as presently known lives in warm seas from 10°N to 30°N, from the Red Sea, Bay of Bengal (India and Thailand), and the Philippine Islands. This is the first report of the egg capsules of *E. costulatum* found on the underside of *Fungia* sp. from the Red Sea. Each egg capsule was encrusted with bits of white coral-sand and attached to another by two slender threads (figure 2). The number of egg capsules per mass is approximately 100.

Root (1958) was the first to report this species as an unidentified epitoniid living under *Fungia*, in the Sulu Archipelago, Philippines. His six specimens are at the Academy of Natural Sciences of Philadelphia (ANSP 230639) and were studied by Robertson (1963) who later (1970) compared them with the holotype in Geneva (original locality unknown) and concluded that Root's specimens are indeed *E. costulatum*. The ANSP speci-

Figure 1. Apertural view of *Epitonium costulatum* (Kiener, 1839). Length 28 mm, width 13 mm, DuShane Collection. Straits of Tiran, Red Sea. **Figure 2.** Coral-sand encrusted egg mass of *E. costulatum*, Chaney Collection. Straits of Tiran, Red Sea. **Figure 3.** *Epitonium ulu* Pilsbry, 1921. Length 13.5 mm, width 5.5 mm, Bratcher Collection. Saudi Arabia, Red Sea. **Figure 4.** *E. ulu* with egg mass. Length of shell 16 mm, width 11 mm, Chaney Collection. Tiran Island, Straits of Tiran, Red Sea. **Figure 5.** Apertural view of *Epitonium bullatum* (Sowerby, 1844). Length 13 mm, width 9 mm, Kaiser Collection. Thomas Reef, Sinai, Red Sea. **Figure 6.** Dorsal view of *E. bullatum*. Kaiser Collection.

mens have 21–26 costae and range in length from 12.4 to 35.3 mm (Robertson, 1963, 1970).

Robertson (1963:60) stated, "There are some wentle-traps which seemingly live throughout most of their post-larval lives with (relatively) large sea anemones (or corals). Such species are . . . *E.* aff. *costulatum* . . . ." "This *Epitonium*, the only wentletrap so far found with a coelenterate other than a sea anemone, presumably feeds on *Fungia*." We now know that *E. costulatum* lays its gelatinous egg masses under *Fungia* on a sandy, rubble substrate, in depths of 2–30 m. Feeding observations are lacking.

Subsequent to 1958, other specimens have been collected from various Indo-Pacific localities.

Recent records: Bay of Bengal, India. One specimen, length 31 mm, with 17 costae and 12 whorls. DuShane Collection.

Raya Island, Bay of Bengal, Thailand. One specimen, length 34.5 mm, with 23 costae and 11 whorls. DuShane Collection.

Phuket Island, SW Thailand. Collected by fishermen under "hat" coral, 15–20 m, 5/22/85. Three specimens, lengths 23.5, 24.5, 25 mm, with 19, 20, 26 costae and 7, 9, 12 whorls. DuShane Collection.

Phuket Island, SW Thailand. Collected by fishermen under "hat" coral, 15–20 m, 5/22/85. One specimen, length 23.5 mm, with 20 costae and 10 whorls. NHM, L.A. 124505.

Tiran Island (SW), Straits of Tiran, Red Sea (27°57′N, 34°32′E). Collected by Henry Chaney, 10/31/85, SCUBA, 2–5 m in rubble under *Fungia* sp., four specimens, three specimens, Chaney Collection, lengths 13, 20, 29 mm, with 18, 23, 28 costae and 8, 9, 13 whorls; one specimen, DuShane Collection, length 28 mm, with 24 costae and 12 whorls. All Chaney collected specimens were live-taken, two were pink in color, with gelatinous egg masses as described above.

Thomas Reef, Sinai, Red Sea (27°59′N, 34°27′E). Collected by Kirstie Kaiser, 10/30/85, SCUBA, 6.1 m in sand pockets under live, detached *Fungia* sp., one specimen, length 23 mm, with 21 costae and 11 whorls, water temperature 25 °C, live shell attached to coral. Kaiser Collection.

Little Hiva, Maldive Islands. Collected by Henry Chaney, 8/31/86, SCUBA, 1 m reef sand, under *Fungia repanda* Dana, 1846, one specimen, live-taken, length 14 mm, with 20 costae and 11 whorls. DuShane Collection.

Epitonium ulu Pilsbry, 1921
(figures 3, 4, 7–10)

Discussion: *Epitonium ulu* Pilsbry, 1921, a widely distributed species, lives in warm seas from 30°N to 5°S, from the Red Sea, to the Maldive Islands, New Guinea and Hawaii. It is specific to certain species of the stony coral genus *Fungia*. Masses of beige colored egg capsules

are laid on the concave underside of *Fungia* spp. attached to both the coral and to adult *Epitonium*.

Bosch (1965) reported that *Fungia scutaria* Lamarck, 1816, from Kaneoke Bay, Oahu, Hawaii, was infested with both eggs and adults of *Epitonium ulu*. The snails had large amounts of pink tissue containing symbiotic algal cells and nematocysts they had ingested.

Taylor (1977) studied the growth rate of *Epitonium ulu* feeding on the sea anemone *Aiptasia* sp. and found that the intracapsular development time for this species varied from five days to several weeks. She found that after hatching the juveniles added approximately 0.2 mm of shell length per day.

Bell (1982) observed that *E. ulu* produced a "mean of 32 capsules per day, each capsule containing 500–600 eggs." She later stated (Bell, 1985) that "embryos complete intracapsular development in six days at 26–27°C and hatch as planktotrophic veligers."

Epitonium ulu has been collected recently from five localities.

Recent records: Maldive Islands. Robertson (1965) reported an *Epitonium* sp. living in association with *Fungia*. He now identifies the four specimens as *Epitonium ulu* (personal communication, 1986).

Papua New Guinea. Collected by Twila Bratcher, 1980, from under *Fungia* sp. (figure 3), 11 m, water temperature 28 °C, length 16 mm, with 30 costae and 11 whorls. Bratcher Collection, and one specimen, length 12 mm with 30 costae and 12 whorls. DuShane Collection.

Tiran Island (SW), Straits of Tiran, Red Sea (27°57′N, 34°32′E). Collected by Henry Chaney, 10/31/85, SCUBA, 2–5 m, with egg mass, under detached *Fungia* on rubble substrate. Five live-taken specimens, all exuding mucus, were collected. Four specimens, Chaney Collection, lengths 3, 4, 5, 16 mm, with 10, 11, 24, 33 costae and 9, 10, 12, 12 whorls; one specimen, DuShane Collection, length 6.5 mm, with 21 costae and 11 whorls.

Sinafir Island, Saudi Arabia, Red Sea. Collected by Twila Bratcher, 10/30/85, SCUBA, 9 m, with eggs under detached *Fungia*. Two live-taken specimens, lengths 9, 13.5 mm, with 17, 24 costae and 9, 10 whorls. Bratcher Collection.

Thomas Reef, Sinai, Red Sea (27°59′N, 34°29′E). Collected by Kirstie Kaiser, 10/30/85, SCUBA, 6 m, water temperature 25 °C. Attached with eggs to underside of detached *Fungia*, lying in small sand pockets with sand and light rubble. Four live-taken specimens, lengths 6, 8, 15, 19 mm, with 17, 20, 23, 32 costae and 10, 10, 13, 14 whorls, all exuding mucus when collected. Kaiser Collection.

All three SCUBA divers (Bratcher, Chaney, Kaiser) collected egg masses (figures 4, 8–10) associated with specimens of *Epitonium ulu* from the Red Sea. The eggs were off-white with light purple spots. One egg sac contained 400–600 embryos in different stages of development. Each translucent egg sac within the cluster is papillose over the entire external surface. The papillae are softly rounded. From each egg sac three transparent twisted threads are attached at each end of the oval egg

.113 mm
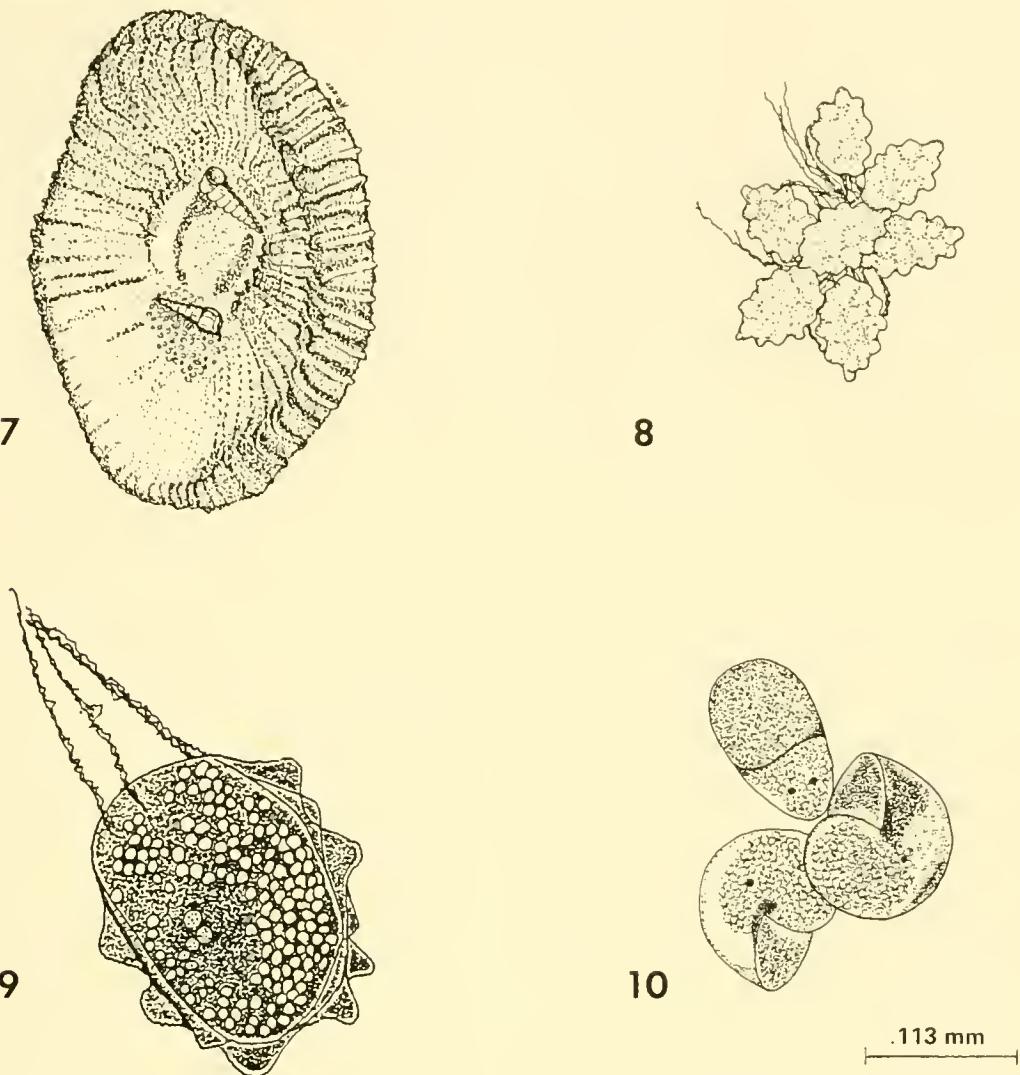
Figure 7. *Epitonium ulu* Pilsbry, 1921 with egg masses on concave underside of *Fungia* sp. **Figure 8.** Egg capsules of *E. ulu* that appear to be empty and transparent. **Figure 9.** Developing, opaque embryos of *E. ulu* located on the inner surface of the transparent sac. **Figure 10.** Prehatching veligers of *E. ulu*. Diameter of a single snail 0.113 mm.

sac, and eventually twist together to form a single knotted mass. Each connecting thread appears to be many times the length of the sac itself.

The egg capsules examined under a microscope (300×) showed the young capsules in three different stages of development. Within each capsule development was uniform. The first stage capsules appeared to be empty and transparent (figure 8). The second stage showed developing, opaque, white embryos that appeared to be located on the inner surface of the sac, but not filling the entire compartment (figure 9). The third stage consisted of well-developed veligers, thus crowding the capsule (figure 10). One capsule in the third stage of development contained 400–600 free swimming veligers of equal size and development. The diameter of a single veliger was 0.113 mm. The gibbous shell is transparent except for the darkened area of the columella. In each embryonic

shell the animal appeared as a uniform gelatinous mass with two dark spots.

Epitonium (Globiscala) bullatum (Sowerby, 1844) (figures 5, 6)

Discussion: *Epitonium (Globiscala) bullatum* (Sowerby, 1844) lives in warm seas from 35°N to 30°S, from the Red Sea, East Africa, New Guinea, Australia, the Philippines, and Japan. Kilburn (1985:330–331) reported this variable species from off Southern Mozambique, and in addition to living under species of *Fungia*, "under rocks in low tide pools, associated with the actinian *Pseudactinia flagcllifera* (Hertw.) on which it feeds; on occasion it may be partly covered by the basal disk of the anemone. Juvenile *bullatum* shelter among coralline algae, probably feeding on the small anemones that are at-

tached to the fronds." He synonymized *Scala* (*Globiscala*) *papyracea* de Boury, 1912 from Natal, *Epitonium* (*Globiscala*) *woolacottae* Kerslake, 1958 from South Queensland and *Globiscala kashiwajimensis* Azuma, 1962 from Japan with *E. bullatum* (Sowerby, 1844).

Recent records: Thomas Reef, Sinai, Red Sea (27°59'N, 34°27'E), collected by Kirstie Kaiser, 10/30/85, SCUBA, 6.1 m, water temperature 25 °C, one live specimen from under live, detached *Fungia*, length 13 mm, with 40 almost imperceptible costae, 7 whorls, protoconch whorls lost, spiral striations weak when viewed under a microscope (10×), umbilicate, color white. A second live specimens was eaten by a wrasse (Labridae), before it could be collected. An egg mass was observed and photographed with this species but not collected.

New Guinea. Three specimens in the DuShane Collection (*ex* Withrow Collection), taken in 30 m, lengths 11, 11.5, 13 mm, with 8, 9, 9 whorls.

Epitonium sp.

An unidentified species of *Epitonium* was reported taken from under *Fungia paumotensis* (Stutchbury, 1833) off Saudi Arabia in the Red Sea by Sabelli and Taviani (1984). Three specimens in varying growth stages were collected with an egg mass at a depth of 2 m. The authors described their specimens as umbilicate with a very thin shell, 22 obsolete costae and interspaces crossed by fine spiral grooves. This is similar to the description of *Epitonium ulu*, but comparison with *E. ulu* is needed.

The extensive paper by Jousseaume (1911) treating 58 species of epitoniids from the Red Sea is of little help in identifying species from that area. Unfortunately, his figures are too small to be of value, and some of his descriptions are vague.

CONCLUSIONS

With an upper surface exposed to the light and a protected concave under surface, species of the genus *Fungia* serve as host for several species of epitoniids with very delicate shells, thin, fragile walls, and numerous costae that are easily shattered. Whether the wentletraps feed on the mucus from the host polyps or the polyps themselves is unknown. Taylor (1975) concluded that *Epitonium ulu* can, under laboratory conditions, feed on the sea anemone *Aiptasia*. All other evidence indicates that *E. ulu* deposits eggs only under *Fungia*. The coral is used as the spawning site, the eggs being laid in gelatinous masses, each capsule connected to another by two threads. The ability of these epitoniids to locate and utilize the underside of Fungiidae requires further study. An increasingly high degree of specificity is being found with certain epitoniids seemingly having permanent associations with *Fungia* corals.

ACKNOWLEDGEMENTS

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A New Species of *Vasum* (Gastropoda: Turbinellidae) from off Somalia

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ABSTRACT

Vasum stephanti new species is described from moderately deep water off Cape Gardafui (Ras Asir), Somalia and compared with congeners.

INTRODUCTION

In the past few years, deep-sea commercial fisheries operations off the northeastern coast of Somalia have resulted in the discovery of several new or otherwise interesting species of mollusks. Lorenz (1987:11) described *Pseudosimnia wieseorum* new species from the region off Cape Ras Hafun in about 300 m, and recorded the presence of *Festilyria festiva* (Lamarck, 1811), *Strombus oldi* Emerson, 1965, and *Cypraea broderipii* Sowerby, 1832, from the trawl samples. Waller (1986:39–46) described *Somalipecten cranmerorum* new genus, new species, from "off Somalia, depth 150–300 m", obtained from Taiwanese fishermen, and also provided a list of associated species. Another species recently described from off Somalia is *Volutocorbis rosavittoriae* Rehder, 1981.

Through the good offices of John Bernard, our attention was called to an unnamed species of *Vasum* trawled in Somalian waters. We take pleasure in describing this new species in honor of Adolphe Stephant, who obtained the specimens from Danish shrimpers and generously provided Mr. Bernard with the data and specimens. Other species of mollusks reported by Mr. Stephant (*in litt.*, August 19, 1987) to have been taken during these trawling operations include *Festilyria festiva*, *Strombus oldi*, *S. plicatus* (Röding, 1798), *Phalium microstoma* (von Martens, 1901), *P. bituberculosum* (von Martens, 1903), *Ficus investigatoris* (E. A. Smith, 1894), *Cymatium ran-*

zanii (Bianconi, 1851), *Bufonaria fernandesi* Beu, 1977, *Vasum crosseanum* (Souverbie, 1875), *Tudicula zanzibarica* Abbott, 1958, *Metula boswellae* Kilburn, 1975, *Cucullaea labiata* (Lightfoot, 1786), and *Chlamys townsendi* (Sowerby, 1895).

SYSTEMATICS

Family **Turbinellidae** Swainson, 1840
Subfamily **Vasinae** H. & A. Adams, 1853

Genus *Vasum* Röding, 1798

Remarks: See Abbott (1959) and Vokes (1966) for reviews of this subfamily.

Vasum stephanti new species
(figures 1–6)

Diagnosis: Similar to *Vasum tubiferum* (Anton, 1839) in general appearance, but differs in having a more triangular outline, three equally well-developed columellar plaits (in place of three major, plus one or two minor plaits), a nearly uniformly milk-white shell with a white, glazed aperture and parietal wall (compared to an orange-brown to yellowish shell with the parietal wall a light tan with very large splotches of chestnut to purple-brown), and in the presence of two or three rows of spines at base of shell (instead of one row).

Description: Shell moderately large for genus, attaining 108+ mm in length. Solid, heavy, turbinate, and strongly spined. Spire elevated with a short, smooth, bulbous nucleus of 1½ whorls (figures 5, 6). Postnuclear whorls 7 (adult specimens lack complete spires), the body whorl with 7 to 8 well-developed, curved to strongly recurved, flaringly grooved and terminally open, subsutural spines.

→

Figures 1–6. *Vasum stephanti* new species. **1, 2.** Paratype, AMNH 225988. **3, 4.** Holotype, AMNH 225987. **5, 6.** Paratype, AMNH 225989 (details of spire). All from type locality: off Cape Gardafui, Somalia, see text; figures 1–4 approximately × ⅔. figures 5, 6, × 2.

A row of similar but much shorter spines below the first row, followed by 5 coarse spiral cords and intervening raised lines. Base of shell with 2 to 3 spiral rows of moderately developed, groove spines and lower surface with weakly developed spiral lines. Parietal wall thickened, slightly raised, glazed. Columella with 3 plicae, posterior 2 better developed; first posterior plica semibifid in 1 specimen. Outer lip moderately thin, slightly reflected, crenulated. Umbilicus funnel-shaped and in most specimens widely open. Base color of shell milky white, spire stained buff. Columella glazed. Aperture white, with a slight bluish tinge. Periostracum moderately thick, tannish brown, and somewhat foliaceous. Soft parts not seen. Operculum brown, corneous, unguiculate, apically nucleate, filling most of the aperture with foot fully withdrawn. Inner surface marginally thickened on basal and abcolumellar sides, central area depressed and with irregular concentric rings; outer surface scabrous.

Type locality: 13–16 km east, 80–96 km south of Cape Gardafui (Ras Asir), Somalia, trawled by shrimp fisherman in 183 to 220 m, December, 1986.

Range: Known only from the type locality and in the Gulf of Aden off the Bari coast of Somalia.

Material examined: Holotype, AMNH 225987, 102.36 mm, *ex* E. Schelling Collection (figures 3, 4); paratype 2, AMNH 225988 (figures 1, 2), paratype 5, AMNH 225989 (figures 5, 6), paratype 8, AMNH 225990, *ex* J. Bernard Collection; paratypes 1, 3, 4, 7, 9 J. Bernard Collection; paratypes 6, 10 A. Stephant Collection, all from the type locality; referred specimen, H. Lee Collection, Alula, Bari coast, Somalia (see Table 1).

Remarks: As noted above, *Vasum stephanti* new species most closely resembles in shell morphology the endemic Philippine (Cuyo-Palawan group) species *V. tubiferum* (Anton, 1839:70; Kobelt, 1876:155, pl. 9, fig. 3; Abbott, 1959:20, pl. 4, fig. 1; Springsteen & Leobrera, 1986:105, pl. 28, fig. 6). Anton's taxon and the closely related *V. turbinellus* (Linné, 1758:750; Abbott, 1959:17, pl. 1, figs. 2, 3), which ranges from East Africa to the western Pacific, are inhabitants of shallow water, as are the other four Indo-Pacific species assigned to *Vasum* (*sensu stricto*) by Abbott (1959). One of these, *V. rhinoceros* (Gmelin, 1791), from Kenya and Tanzania, is somewhat similar but has a lower-spired, heavier shell with massive nodules, thickened and reflected outer lip, and a brown-blotched to light yellow parietal wall (Abbott, 1959:21, pl. 4, figs. 3, 4). Strongly spinose specimens with immature outer lips of the Brasilian *V. cassiforme* (Kiener, 1840), cited from low tide to 60 m (Rios, 1985:115), are superficially similar to the new species. (See Abbott & Dance, 1982:209, 210 for polychrome illustrations of these taxa.) The Australian *Altivasum* Hedley, 1914, and several species of Indo-Pacific *Tudicula* H. & A. Adams, 1864 are known to occur in moderate depths (to 220 m).

   Some of the spinose species originally assigned to *Tudicula* (*e.g.*, *T. zanzibarica* Abbott, 1958, from the western Indian Ocean, and *T. rasilistoma* Abbott, 1959), from

Table 1. *Vasum stephanti* new species. Shell measurements in mm and number of whorls; width measured including spines. n = 12. Spires incomplete except for 5, 10.

	Length	Width	# Whorls
Paratype 1	107.68	97.88	6
Paratype 2	106.75	97.11	6
Holotype	102.36	82.70	6
Paratype 3	97.72	82.08	6
Paratype 4	97.10	84.19	6
Paratype 5	95.53	77.93	8½
Paratype 6	86.22	73.47	6
Paratype 7	78.75	64.10	5
Paratype 8	73.68	57.18	5
Paratype 9	66.87	67.25	5
Referred	63.47	52.78	5
Paratype 10	56.92	55.79	4½

off Queensland, Australia, may prove to be referable to *Vasum* when the soft anatomy is known. The weakly spinose *V. crosseanum* (Souverbie, 1875), from the Indian Ocean, appears to be closely related to *T. rasilistoma*. The development of long spines in the species described herein may reflect the deeper-water habitat.

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Density, Spatial Distribution, Activity Patterns, and Biomass of the Land Snail, *Geophorus bothropoma* Moellendorff (Prosobranchia: Helicinidae)

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ABSTRACT

The results of preliminary work done in the Republic of the Philippines during July, 1981 on the density, spatial distribution, activity patterns, and biomass of the Philippine Island land snail *Geophorus bothropoma* (Prosobranchia, Helicinidae) are presented

Density was estimated at $0.55/m^2$ utilizing the quadrat method. Using the parameters of mean crowding and patchiness, the species was shown to be uniformly distributed spatially, possibly due to mutual repulsion. Individual activity distance per 24 hour period varied greatly (0.0–275.0 cm) and was possibly correlated with rainfall. Utilizing the convex polygon and ellipsoid methods, minimum individual activity ranges for the duration of the study were estimated to be 2.4–4.2 m^2. Biomass (live weight) of adults was estimated at 0.13 g/m^2. The species is diurnal and does not home.

Key words: Gastropoda; Prosobranchia; Helicinidae; *Geophorus*; density; spatial distribution; activity; biomass; Philippine Islands.

INTRODUCTION

There are relatively few published studies dealing with the density, spatial distribution, activity patterns, or biomass of land snails (see Discussion section for citations). Of those that do exist, almost all have dealt with pulmonates of temperate regions, while tropical terrestrial prosobranchs remain virtually unstudied. The present paper reports on the results of a preliminary study conducted July 7–17, 1981 on *Geophorus bothropoma* Moellendorff, 1895 (Quadras & Moellendorff, 1895:148; Wagner, 1908:152, pl. 29, figs. 20–23), a large (13.0–16.0 mm in diameter), limestone rock-dwelling helicinid endemic to the Caramoan Peninsula, Luzon. This represents one of the very few times quantitative ecological methods have been utilized for the study of terrestrial mollusks in all of Southeast Asia. In addition, the present paper introduces to ecological malacology several analyses used by zoologists working in groups other than mollusks (*i.e.*,

birds, Odum & Kuenzler, 1955; frogs, Turner, 1960; insects, Alexander, 1961, Iwao, 1970; mammals, Stumpf & Mohr, 1962). While the database with which we worked was rather small, the ease of analyses and the applicability of the results suggest that such approaches to similar questions in terrestrial snail ecology would be highly beneficial.

STUDY AREA

The study area is located in the Republic of the Philippines, Luzon Island, Camarines Sur Province, Caramoan Municipality, 1.0 km south of Barrio Ilawod. The work was conducted 10 m off the trail between Ilawod and Gota Beach on a large (8 × 9 × 3 m high) limestone boulder with almost vertical sides.

Much of the Caramoan Peninsula consists of well-developed limestone karst of Miocene reef origin. Because the area has been relatively recently uplifted, the mountains are rather steep. Hills and ridges often consist of masses of large limestone boulders with chasms tens of meters deep. Runoff is rapid and though rainfall may be high seasonally, the surface environment is often relatively dry. Surface water collects in solution pits on limestone and in hollows of trees.

Due to the rugged topography, the area remains blanketed in a multi-canopied, tropical evergreen forest. Vegetational communities are extremely diverse. The forest is dominated by tall dipterocarp trees in both upper (30–40 m) and lower (5–20 m) canopies; a dense herbaceous layer of mainly ferns exists near the ground surface.

The Caramoan Peninsula has no definite dry season. While it tends to rain throughout the year (ca. 2,900 mm), most rainfall occurs from September through January, with a minor peak in July associated with the onset of the typhoon season.

As in other tropical rainforests, the Caramoan Peninsula shows little seasonal temperature variation. Mean

daily temperature fluctuations are greater than mean seasonal variation. However, there is a marked vertical thermocline within the forest, in which temperatures from the surface to 1 m are most stable; daily variation increases at greater heights above the ground. Due to the dense vegetation at the study site, the effects of solar radiation and wind are minimal. Therefore, *Geophorus bothropoma* lives in the most stable part of the local warm, moist tropical forest environment. The above ecological data is from Auffenberg (in press).

METHODS

An 8 m² (2 m tall, 4 m wide) vertical grid of 1 m² quadrats was constructed against the east side of the boulder to measure density and activity. All adult *Geophorus bothropoma* within this grid ($N = 14$) were numbered with small dots of fingernail polish on the dorsal surface of the shell. This increased shell visibility, but is not believed to have increased predation due to the nocturnal habits of most potential predators. No additional individuals were located during subsequent visits. The site was visited nine times during the next 11 days at 10 A.M. for approximately 1 hour observations. In addition, the site was visited sporadically throughout the daylight hours and seven times at night (8–10 P.M.). This provided a set of successive censuses, not a random quadrat sampling.

Density estimates are based on the quadrat sampling method. This method simply involves counting individuals occurring within a quadrat of fixed size.

Analyses of spatial distribution are based on m* (mean crowding) and m*/m (patchiness) of Lloyd (1967). Mean crowding is given by the formula:

$$m^* = \frac{\sum_{j=1}^{q} x_j^2}{\sum_{j=1}^{q} x_j} - 1 \qquad (1)$$

where x_j = the number of individuals in the jth quadrat and q = the total number of quadrats.

Mean crowding is defined as the mean number of other individuals per quadrat per individual. It expresses the degree of spatial crowding experienced by an individual because of others of the same species (or different species; see Lloyd, 1967). A particularly important feature of this statistic is that it is relatively independent of spatial distribution type, number of samples, and size of the means. The most complete discussion concerning the utility of this statistic is by Iwao (1977). It should be stressed that this statistic does not measure crowding in an ecological sense, as many variables (*i.e.*, food availability, territoriality) must be examined before this can be determined (Lloyd, 1967).

Patchiness (m*/m) is the ratio of mean crowding to mean density (Iwao, 1968). This index provides a relative measure of aggregation. It equals unity (1) in random distribution, is greater than unity in contagious distributions and is less than unity in regular (uniform) distributions (Iwao, 1977).

Analysis of the activity of *Geophorus bothropoma* was made by subdividing the 1 m² quadrats, plotting the exact location of individuals and measuring straight line distances (nearest cm) from the last observation with a flexible tape. This provided a crude estimate of the minimum distance traveled since the last observation. Calculations are based only on data provided by two or more consecutive daily observations ($N = 27$).

Estimations of activity ranges ($N = 5$) are based on the convex polygon method and the ellipsoid method, which is based on a covariance matrix of capture loci (Jennrich & Turner, 1969). The convex polygon method involves plotting all the recapture points, drawing the smallest convex polygon containing these points and then determining the area. This method, defined by the equation:

$$A = \frac{x_i y_{i+1} - x_{i+1} y_i}{2} \qquad (2)$$

is relatively simple but is biased by sample size. The values tend to increase as the number of capture points increases.

The ellipsoid method is not biased by sample size and assumes that individuals are active outside the observed range of activity (see Jennrich & Turner, 1969, for discussion). This method is defined by:

$$A = 6\pi |S|^{\frac{1}{2}} \qquad (3)$$

where $|S|$ is the determinant of the capture point covariance matrix;

$$S = \begin{bmatrix} S_{xx} S_{xy} \\ S_{yx} S_{yy} \end{bmatrix} \qquad (4)$$

defined by the equations;

$$S_{xx} = \frac{1}{n-2} \sum_{i=1}^{n} (x_i - \bar{x})^2,$$

$$S_{yy} = \frac{1}{n-2} \sum_{i=1}^{n} (y_i - \bar{y})^2,$$

$$S_{xy} = S_{yx} = \frac{1}{n-2} \sum_{i=1}^{n} (x_i - \bar{x})(y_i - \bar{y}),$$

$$\bar{x} = \frac{1}{n} \sum_{i=1}^{n} x_i,$$

$$\bar{y} = \frac{1}{n} \sum_{i=1}^{n} y_i \qquad (5)$$

Live adult snails ($N = 90$) were collected near the study site and their weights (in groups of 10 individuals) were taken to the nearest milligram on a single beam, double pan scale. Fifty specimens were then macerated; the shells and opercula were rinsed, dried for several days and reweighed.

Voucher specimens of *Geophorous bothropoma* are housed in the mollusk collection of the Florida State Museum (UF 56667).

Table 1. Density and spatial distribution parameters based on quadrat method. n = individuals recaptured per visit, m/m² = density, m* = mean crowding, m*, m = patchiness. Visit 6 is omitted from density and spatial distribution analyses.

	Visits									$\bar{x}$	SE	SD
	1	2	3	4	5	6	7	8	9			
n	9	6	5	5	2	0	1	3	4	3.89	—	—
m/m²	1.13	0.75	0.63	0.63	0.25	—	0.13	0.38	0.50	0.55	0.11	0.32
m*	1.11	1.00	0.40	1.20	0.00	—	0.00	0.67	0.00	0.55	0.18	0.52
m*/m	0.98	1.33	0.64	1.90	0.00	—	0.00	1.76	0.00	0.83	0.28	0.79

RESULTS

Density and spatial distribution: Pronounced variation in population density was observed during this study (table 1). Densities were calculated in eight quadrats for nine visits (N = 72 quadrats). Visit 6 yielded no recaptures and is omitted from density and spatial distribution analyses. Depending on the individual visit analyzed, mean crowding and patchiness reveal either random, contagious, or uniform spatial distributions. However, the means of these statistics suggest that individuals are uniformly distributed, for the averages of both mean crowding *and* patchiness are less than unity.

The regression of mean crowding on mean density (figure 1) also suggests a uniform spatial distribution (α = y intercept = -0.14, β = slope = 1.25) with possible "mutual repulsion" (see Iwao, 1968, for discussion of regression analysis).

Activity: Marked individuals were observed to be active during all daylight hours. None were active during visits after dark. A typical activity sequence consisted of an individual moving along a meandering path for several minutes, sometimes feeding on algal growth, stopping for several minutes, then continuing. Some individuals remained at the same exact location for 1 or 2 days, while for no apparent reason others remained active.

Fifty-seven recaptures were recorded (50.9% of possible recaptures). Distances traveled per day varied greatly between individuals (0.0–275.0 cm). Because distances traveled rarely conform to normal distributions only the range of distances is given.

Population activity variation was possibly correlated with rainfall. Light rain did not initiate activity in inactive individuals, nor did it seem to affect individuals already active. However, snails ceased moving about if the rainfall became intense. Above average activity levels were observed between July 8 and 11 (50.0–275.0 cm, N = 11 recaptures, three visits) following intense rainfall associated with two small typhoons in the area. This in turn was followed by 5 days (July 12–16) of relatively little rainfall and reduced snail activity (0.0–65.0 cm, N = 10 recaptures, four visits). A heavy rain fell during the night of July 16, resulting in a marked increase in snail activity on July 17 (65.0–203.0 cm, N = 6 recaptures, one visit).

Perhaps the most interesting observation concerning the activity of this species is that it does not home. Individuals simply wander from one resting site to another, usually shallow depressions or crevices in the rock. They avoid resting sites in leaf-filled solution pits, which are, however, usually inhabited by *Cyclophorus ceratodes* Moellendorff, 1895, *Japonia ciliata* (Sowerby, 1843), *J. stephanophora* (Moellendorff, 1895), and several small pulmonate species (personal observation).
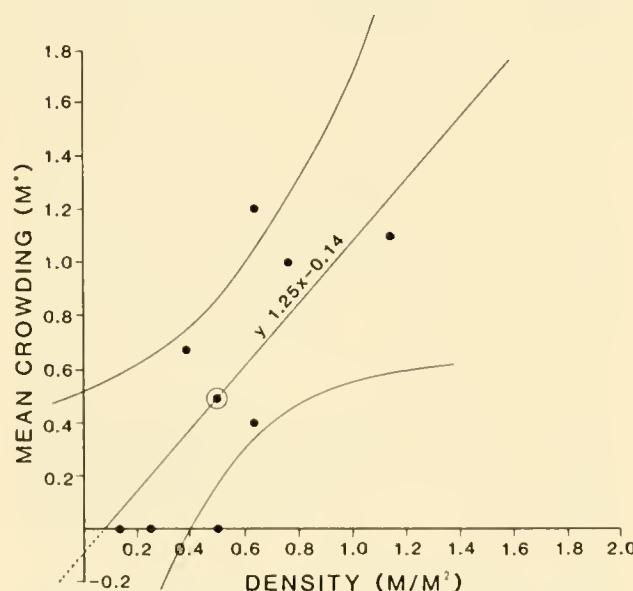
Figure 1. Regression of mean density (m/m²) on mean crowding (m*) of *Geophorus bothropoma* in study area. Curved lines represent 95% confidence limits.
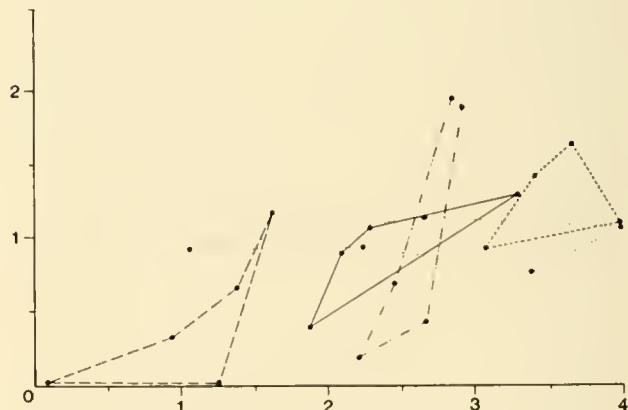
Figure 2. Five representative activity ranges of *Geophorus bothropoma* plotted on 8 m² grid. Black dots represent recapture sites. Each polygon depicts an activity range of an individual snail over an 11 day period.

Estimates of individual activity ranges (N = 5) (figure 2) are quite consistent. The convex polygon method (corrected for sample size bias; Jennrich & Turner, 1969) yielded activity ranges of 2.3–3.8 m² ($\bar{x}$ = 3.1 ± 0.3, SD = 0.5 m²). The ellipsoid method yielded slightly (but insignificantly), larger area estimates of 2.7–4.2 m² ($\bar{x}$ = 3.3 ± 0.3, SD = 0.6 m²).

Biomass: Mean total live weight per adult individual in the study area was 0.59 g (N = 90). Mean shell weight (including operculum) per individual was 0.35 g (N = 52), yielding a mean live biomass per individual of 0.24 g. The mean density estimated by the quadrat method (table 1) of this species in this area is 0.55 individuals/m². Thus the estimated biomass is 0.13 g/m².

DISCUSSION

Density and spatial distribution: Previous studies on species comparable in size to *Geophorus bothropoma* have been few (*i.e.*, Mason, 1970; Richardson, 1975; Cameron, 1982), and none concerns terrestrial prosobranchs. The only prosobranchs with available data are the small hydrocenid *Georissa monterosatiana* (Godwin-Austen & Nevill, 1879) and the diplommatinid *Opisthostoma retrovertens* Tomlin, 1938 of Malaysia. Berry (1966) found these species occurring in higher densities on moss covered rocks than on moss-free rocks, but did not address spatial distribution. In the Caramoan area we found *Georissa rufescens* (Moellendorff, 1887) in extremely localized and highly aggregated populations on vertical rock faces. This is very different from the large *Geophorus bothropoma*, which is found on virtually every vertical rock face and is uniformly distributed spatially.

In this study, intersample variation in estimated mean densities is probably largely due to the limited size of the study area. The choice of study area size and number of samples must have some biological basis to estimate population density and spatial distribution adequately. This is usually done by preliminary sampling or guessing (Iwao, 1977). However, we do feel confident that the proper quadrat size (1 m²) was chosen because the observed daily activity was approximately 1 m ($\bar{x}$ = 93.7 ± 13.31 cm). Density estimates were possibly also biased by the rugged microhabitat. The limestone karst provides many cracks, crevices, and solution pits in which a snail could remain unseen, despite our thorough searches.

Utilizing Iwao's (1968) interpretation of m*/m regressions, we determined that individuals of *Geophorus bothropoma* were uniformly distributed and may have exhibited "mutual repulsion." Infra-specific competition has never been properly substantiated in studies on terrestrial mollusks and we cannot substantiate it here. Nevertheless, density was relatively low, despite the seemingly adequate food and resting site resources that could have been expected to sustain substantially higher snail densities.

Activity: Previous studies have shown terrestrial mollusks to be very cyclic in their activity patterns (*i.e.*,

Barnes & Weil, 1944, 1945; Wells, 1944; Dainton, 1954a,b; Blinn, 1963; Henne, 1963; Cameron, 1970; Crawford-Sidebotham, 1972; Baker, 1973; Bailey, 1975; Shachak *et al.*, 1975; Heatwole & Heatwole, 1978; Deisler, 1987). It is apparent from these studies that the initiation and continuation of activity is a variable response to complex, simultaneous climatic changes (some minute, perhaps immeasurable) in the microenvironment. More field and laboratory studies must be undertaken before this will be understood. In previous studies snail movements were most numerous shortly before or after nightfall and shortly before dawn. However, *Geophorus bothropoma* is diurnal rather than crepuscular, and the congener *G. trochiformis* (Sowerby, 1842) was also observed active throughout the day. We believe this behavioral pattern is not a general trend in tropical terrestrial prosobranchs. *Cyclophorus ceratodes* Moellendorff, 1895 and *Japonia ciliata* (Sowerby, 1843) and *J. stephanophora* (Moellendorff, 1895) living in the same study area are decidedly crepuscular in their activity patterns (personal observation).

Few data are available on activity and home site ranges of terrestrial mollusks. Heatwole and Heatwole (1978) found individual home site ranges of the camaenid *Caracolus caracollus* (Linne, 1758) to vary greatly (0.08–59.0 m²). Since *Geophorus bothropoma* does not home we prefer to call the area enclosed by the recapture sites (figure 2) the activity range. The term homesite range implies that the individual possibly returns to a certain area after foraging outside that area. We assume that the activity range of *Caracolus caracollus* is much larger than the enclosed polygon determined by recapture sites.

Long-term study is needed to provide a meaningful estimate of the activity range of *Geophorus bothropoma*. The data presented here only provide an estimate of the minimum size of the activity range expected during a wet part of the year. Activity ranges are probably significantly smaller during the dry season.

Homing is apparently based on chemoreception (see Cook, 1979, for review). The advantages and/or disadvantages of homing have not been properly addressed. A permanent resting site should provide relative safety from predators and fulfill the physiological requirements of the individual at rest. The physiological and/or behavioral basis for *Geophorus bothropoma* being unable to (or not having to) home is not known. Although the operculum provides protection from small predators and desiccation, this does not explain this species' lack of homing behavior. *Geophorus bothropoma* most commonly rests on vertical rock faces. Even when inactive, it does not retract fully into the shell, leaving the operculum non-functional. Because *Cyclophorus ceratodes* Moellendorff, 1895 and *Japonia ciliata* (Sowerby, 1843) and *J. stephanophora* (Moellendorf, 1895) were found to return to the same solution pits after foraging (personal observation), non-homing is not a general trend in tropical terrestrial prosobranchs.

Biomass: Few data on the biomass of terrestrial mollusks are available (Strandine, 1941; Jennings & Bark-

ham, 1975; Richardson, 1975; Cameron, 1982) and none concern prosobranchs, nor do they provide easy or direct comparisons. Many more species must be studied before general trends can be demonstrated.

Fragments of one marked specimen were found in a solution pit, possibly preyed on by the nocturnal shrew, *Suncus marinus* (Linne, 1766), an introduced species. This species was seen on two occasions at the study site. Many shells of *Geophorus bothropoma* gnawed open at the periphery were found in solution pits nearby. The diurnal, snail-eating monitor lizard *Varanus grayi* Boulenger, 1885 rarely preys on this species (Auffenberg, in press).

Although short-term data such as those presented here add much to our knowledge of this species, only with long-term life-history studies will questions be answered with confidence. Combined with morphological information, sound behavioral and ecological data will undoubtedly contribute greatly to a better understanding of the systematics and evolution of Philippine helicinids.

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THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

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CONTENTS

The Egg Capsules, Embryos, and Larvae of *Cancellaria cooperi* (Gastropoda: Cancellariidae)

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ABSTRACT

The egg capsules, and the embryonic and larval development of the cancellariid gastropod *Cancellaria cooperi* Gabb are described. Egg capsules are spatulate in form, having long, narrow stalks that support the eggs above the surrounding sand. Egg capsules contain 4,000–5,000 eggs (165 μm in diameter), which undergo typical prosobranch development to hatch as planktotrophic veligers after 27 days at 15 °C. Larvae in culture grew from 305 μm to 890 μm in shell length over 30 days, but died before metamorphosis. Limited comparative data suggest that long stalked egg capsules are known only in members of the Cancellariinae, that opercula, absent in all adult Cancellariidae, are present or prominent in the late larval stages of at least some species, and that developmental type cannot be inferred from protoconch morphology using the criteria of Shuto (1974) in a majority of cancellariid species.

Key words: Reproduction; development; larvae; eggs; egg capsules; Cancellariidae; *Cancellaria*.

INTRODUCTION

Little is known about the reproductive biology and early development of most of the approximately 200 species that constitute the neogastropod family Cancellariidae. The few published reports (Mörch, 1869; Thorson, 1935, 1944; Knudsen, 1950; MacGinitie, 1955; Kilburn & Rippey, 1982; Bouchet & Warén, 1985) are limited to descriptions of egg capsules and, in some cases, ova or larval shells attributed to cancellariids, usually on the basis of the proximity of living snails.

During studies of the diet and feeding behavior of *Cancellaria cooperi* Gabb, 1865, a species that is attracted to and specifically parasitizes the Pacific electric ray *Torpedo californica* Ayres, 1855 (O'Sullivan *et al.*, 1987), a number of these snails were observed producing egg capsules. The present study supplements our knowledge of the natural history of this cancellariid with descriptions of its egg capsules and embryonic and larval development, and reviews the available data on the reproductive biology and larval development of the Cancellariidae.

MATERIALS AND METHODS

Twenty-three specimens of *Cancellaria cooperi* were collected on the artificial reef "Torrey Pines #1", off San Diego, CA (32°53'12"N, 117°50'50"W) at depths of 20–22 m using SCUBA. The animals were maintained in an aquarium containing sufficient sand for complete snail burial (4–8 cm depth) and supplied with a continuous flow of seawater (12–16 °C). Snails were allowed to feed on electric rays on a bimonthly basis, and had been maintained in this manner for at least 6 months prior to the onset of oviposition.

Individual egg capsules were freed from the aquarium bottom and maintained in beakers containing continuously aerated, 1 μm filtered seawater at 15 °C. Developing embryos were removed with a glass pipette through an incision cut along the narrow edge of the egg capsule. Hatched larvae of *Cancellaria cooperi* were cultured following procedures described by Paige (1986), except that 1 μm filtered natural seawater containing 40 mg/liter each of the antibiotics streptomycin sulfate and sodium penicillin G was used instead of artificial seawater. Larvae were fed a mixture of the green flagellates *Isochrysis galbana* (Park, 1949) and *Pavlova lutheri* (Droop) Green, 1975 at 10^4 cells/ml. Prior to photography, larvae were narcotized in a 1:3 mixture of a saturated aqueous solution of chlorobutanol in seawater.

Eggs and larvae for SEM examination were fixed in 2% formalin in seawater, and stored in 70% ethanol. Specimens were critical-point dried and photographed using a Hitachi S-570 Scanning Electron Microscope.

RESULTS

Beginning April 21 and continuing through May 19, 1986, a total of 15 egg capsules were laid by at least three snails (mean shell length = 62.3 mm), with nine capsules being produced sequentially by a single female.

Figure 1. *Cancellaria cooperi* Gabb. Apertural and right side view of female specimen collected by SCUBA in 20–22 m at artificial reef "Torrey Pines #1", off San Diego, CA (32°53′12″N, 117°50′50″W), USNM 846054. 1.0 ×.
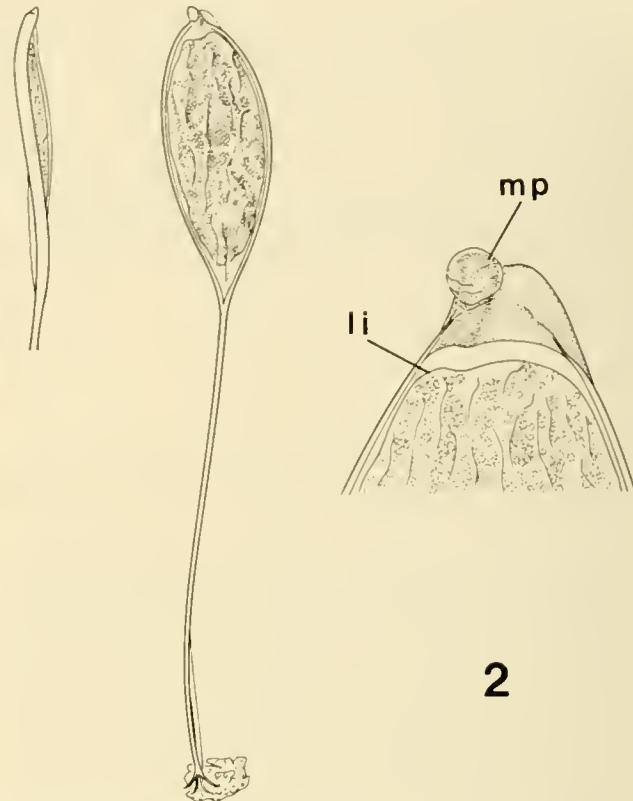
Figure 2. Egg capsule of *Cancellaria cooperi* Gabb. Frontal and side views 1.0 ×, detail of hatching aperture 6.0 ×. mp, mucous plug; li, membranous sack.

Oviposition generally occurred at night or in the morning. Snails emerged partially from the sand, with their raised foot spread anteriorly and enfolded posteriorly, the emerging stalk protruding from the folded portion of the foot. Over the course of several hours, the egg case emerged from the ventral pedal gland and was released, whereupon the stalk straightened and the egg case was supported well above the surface of the sand.

The spatulate capsules (figure 2; table 1) consisted of lenticular egg cases supported on long, narrow (250 μm diameter) stalks. Egg capsules were roughly rectangular in transverse section, with narrow keels running along the outer edge of each corner. A pre-formed hatching aperture, containing a membranous plug (figure 2, mp), was situated at the uppermost end of each egg case. Capsules were affixed to the bottom of the aquarium by holdfasts that spread from the base of the stalk.

Each egg case contained an estimated 4,000–5,000 spherical eggs (figures 3, 4; diameter = 164.5 ± 6.7 μm, N = 10), suspended in a clear, gelatinous matrix, all of

which was enveloped in a membranous, transparent sack (figure 2, li). The lenticular walls of the egg case were slightly concave, creating a constriction along the midline of the case that displaced the eggs to either side.

Spiral cleavage commenced within 12 hours of oviposition, and the 8 cell stage (figure 5) was reached by the second day. Thereafter, the embryos became increasingly irregular in form (figures 6–8). All the embryos within an egg case underwent development; there were no nurse eggs or unfertilized eggs in the cases examined. By 10 days after deposition, the stomodeal invagination was evident (figure 9). After 12 days, the protoconch and operculum, both of conchiolin, were clearly discernable (figures 10, 11), and torsion was complete after 14 days (figures 12–14). The velar lobes were formed and increasing in size by the 16th day (figures 15, 16). On the

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Figures 3–14. Embryonic and larval development of *Cancellaria cooperi* Gabb at 15 °C. **3.** Living embryos, 1 day old. **4.** One-day-old embryo, critical-point dried. Scale bar = 25 μm. **5.** Living embryos, 2 days old. **6.** Living embryo, 4 days old. **7.** Four-day-old embryo, critical-point dried. Scale bar = 50 μm. **8.** Living embryos, 8 days old. **9.** Ten-day-old embryo, critical-point dried. Scale bar = 50 μm. **10.** Living embryos, 12 days old. **11.** Right side and ventral views of same 12-day-old embryo, critical-point dried. Scale bar = 50 μm. **12.** Living embryos, 14 days old. **13, 14.** Ventral (13) and dorsal (14) views of 14-day-old embryos, critical-point dried. Scale bar = 50 μm.

asr, apical sensory region; dml, dorsal mantle lip; lk, larval kidney; o, operculum; pb, polar body; pc, protoconch; pt, prototroch; s, stomodeum.
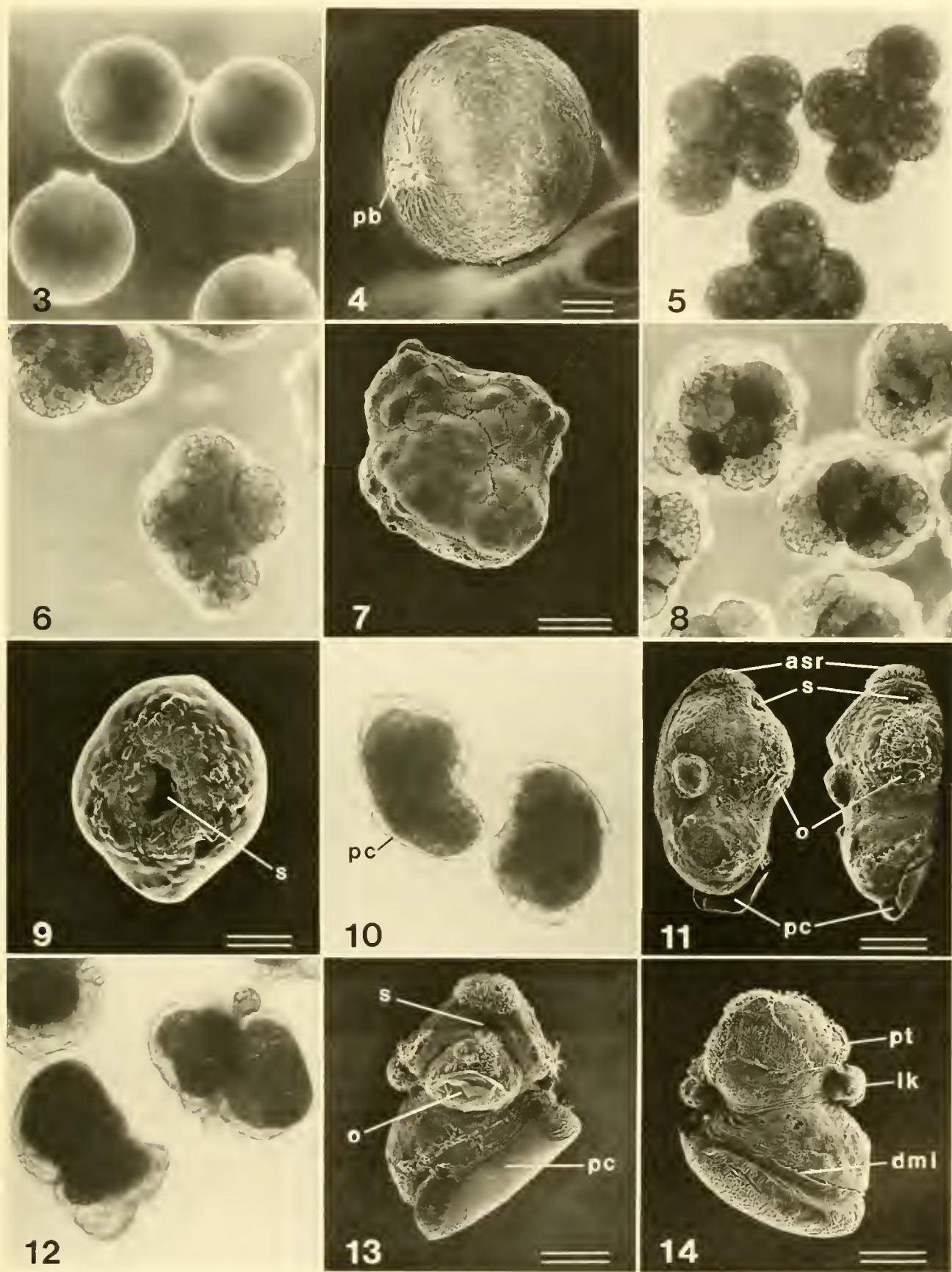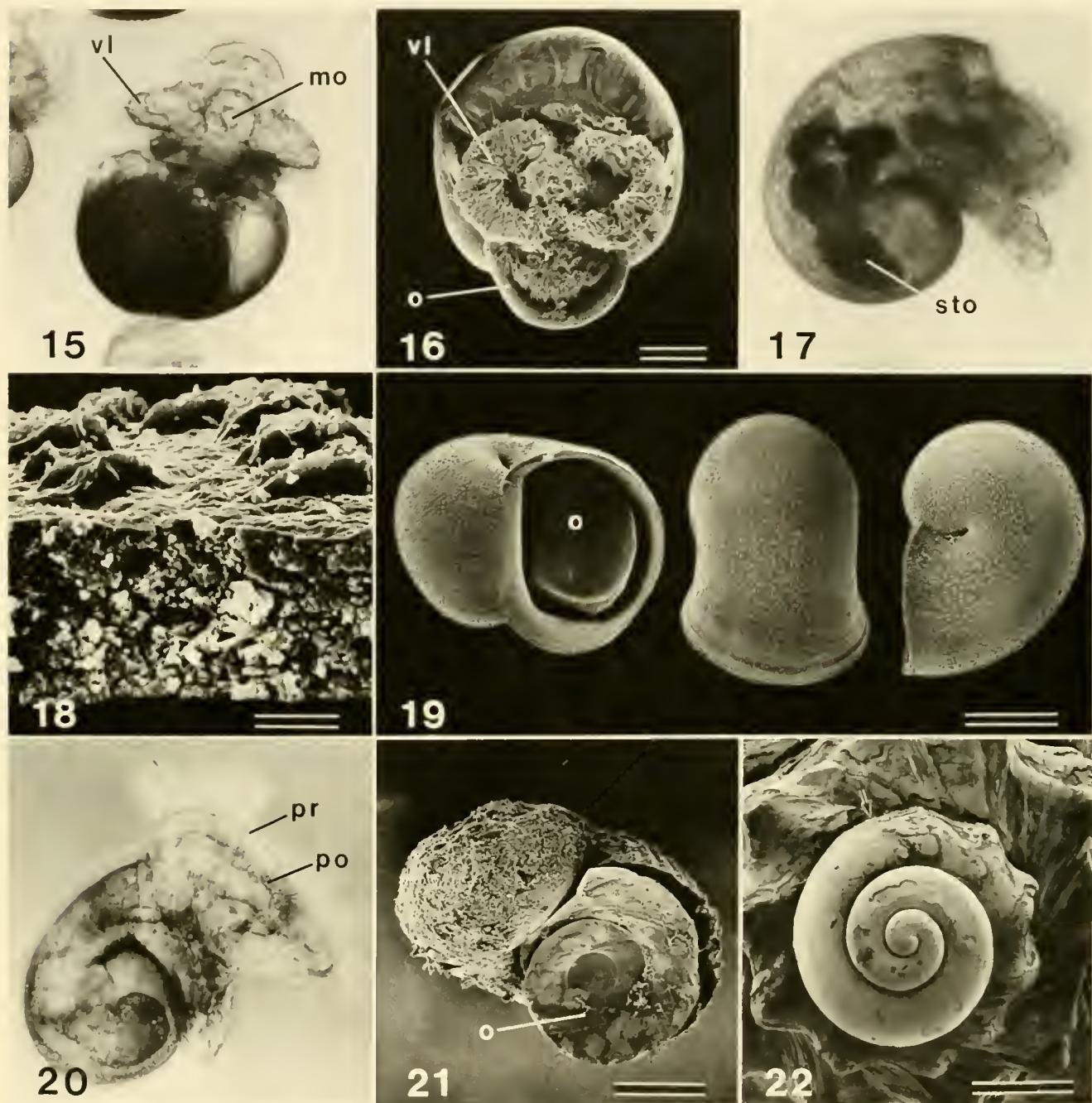
Figures 15–22. Embryonic and larval development of *Cancellaria cooperi* Gabb at 15 °C. **15.** Living embryo, 16 days old. **16.** Sixteen-day-old embryo, critical-point dried. Scale bar = 50 μm. **17.** Living, newly-hatched larva with carmine particles in the gut. **18.** Shell ultrastructure of newly-hatched larva, plane of fracture parallel to growing edge. Scale bar = 2 μm. **19.** Apertural, dorsal and apical views of shells of newly-hatched larvae. Scale bar = 100 μm. **20.** Living larva, 30 days after hatching. **21.** Shell and operculum of larva, 30 days after hatching. Scale bar = 250 μm. **22.** Apical portion of adult shell (LACM 40-95.1), arrow indicating transition from protoconch to teleoconch, scale bar = 500 μm.

mo, mouth; o, operculum; po, posterior ciliary band; pr, preoral ciliary band; sto, stomach; vl, velar lobe.

20th day after capsule deposition, embryos began to move more freely within the egg case. The gelatinous matrix in which the developing embryos had been suspended became less viscous, and the swimming embryos aggregated randomly within the case. After an average of 27 days at 15 °C the membranous plug occluding the hatching aperture dissolved, and swimming larvae escaped. Shells of the newly hatched veligers (figures 18, 19) had a mean diameter of 304.6 μm (N = 10, SD = 3.5), and were 3.9 μm thick. The veligers possessed an operculum

Table 1. Measurements of egg capsules of *Cancellaria cooperi* Gabb. All measurements in mm (N = 10).

Character	Mean	Range	SD
Total length	79.6	70.5–83.6	4.8
Capsule length	30.1	27.8–32.8	1.9
Capsule width	11.4	10.7–12.4	0.6
Capsule thickness	1.8	1.6–2.0	0.2
Stalk length	49.5	37.7–54.0	6.0
Maximum diameter of holdfast	9.1	7.4–10.8	1.2

Figure 23. Relationship of the number of whorls (Vol) and the ratio of maximum diameter to number of whorls (D/Vol) of cancellariid protoconchs. Solid circles denote species for which type of development is known or inferred on the basis of number of ova per capsule. Open circles denote species for which type of development is unknown. 1, *Cancellaria cooperi*; 2, *Trigonostoma foveolata*; 3, *Admete viridula*; 4, *Cancellaria reticulata*; 5, *Cancellaria spengleriana*; 6, *Trigonostoma scalare*; 7, *Olssonella smithii*; 8, *Narona mitraeformis*; 9, *Scalptia obliquata*; 10, *Cancellaria similis*.

(figure 19, o), and a fully functional alimentary system. When added to a small dish of seawater containing suspended carmine particles, the veliger larvae rapidly filled their guts with these particles (figure 17, sto).

Attempts to rear these veliger larvae through metamorphosis were unsuccessful. At 20 °C, larvae grew rapidly, reaching a mean shell diameter of 644 μm (figure 20) 22 days after hatching. Thereafter, the larvae began to die, with only a single larva surviving 30 days after hatching (shell diameter = 890 μm, figure 21). Larvae that had survived more than 22 days after hatching developed propodia, but did not metamorphose in the presence of fresh or frozen *Torpedo* mucus, or in the presence of sand from an aquarium containing adult snails. No crawling or search behavior associated with the onset of metamorphic competence was observed. Protoconchs of adult shells of *Cancellaria cooperi* indicate that the larval shell reaches 3.3 whorls (shell diameter = 1,160 μm) prior to metamorphosis (figure 22; table 2).

DISCUSSION

Egg capsules of *Cancellaria cooperi* resemble those of many neogastropods (*e.g.*, D'Asaro, 1970; Radwin & Chamberlin, 1973; Bandel, 1976), with notable modification in the length of the supporting stalk. This elongation of the stalk appears to be an adaptation for unstable sediments in which capsules are deposited. Under natural conditions, egg capsules are most likely attached to buried stones or shells, with the long stalk supporting the egg case well above the sand surface, preventing its burial, and possibly protecting the eggs from small, bottom-dwelling predators. The compressed, spatulate form of the egg case may serve to increase the surface area available for diffusion of gases and waste products be-

tween the egg case and the surrounding seawater. Capsules were most frequently laid with the broad face of the case oriented into the stream of flowing seawater.

The egg cases of *Cancellaria cooperi* are most similar in morphology to those reported by Knudsen (1950: fig. 18) for *Cancellaria* sp., and to his account of the egg cases of *Cancellaria spengleriana* (Deshayes, 1830). All have the characteristic long stalk, but the latter two are described or figured as being hemi-elliptical rather than lenticular in profile, and triangular rather than rectangular in transverse section. Egg cases of *Trigonostoma foveolata* (Sowerby, 1848), a species occurring "in sand or gravel among rocks in low-tide pools", are similar to those of *Cancellaria cooperi* in shape, but are smaller in size, and have a proportionally shorter stalk (Kilburn & Rippey, 1982:115). Capsules of *Admete viridula* (Fabricius, 1780), a subtidal boreal species, are attached directly to the substrate and lack a stalk [Thorson, 1935: fig. 71

Table 2. Protoconch measurements of the three cancellariid species for which the mode of development is known or inferred based on number of ova per capsule. Measurements are presented in the format mean/standard deviation. D = diameter in mm; Vol = number of whorls or volutions, measured according to Jablonski and Lutz (1980:332).

Species	D	Vol	D/Vol
Cancellaria cooperi: LACM 40-95.1; LACM 39-94.1; LACM 39-116.2 (N = 4)	1.16/0.02	3.29/0.02	0.35/0.01
Trigonostoma foveolata: NM C8393; NM C8394; NM B7651 (N = 5)	1.33/0.21	2.24/0.21	0.59/0.08
Admete viridula: USNM 189720 (N = 10)	0.78/0.05	2.12/0.10	0.37/0.01

Table 3. Protoconch measurements for cancellariid species for which mode of development is not known. Data are presented in the format of mean/standard deviation. D = diameter in mm; Vol = number of whorls or volutions, measured according to Jablonski and Lutz (1980:332).

Species	D	Vol	D/Vol
Cancellaria reticulata: USNM 619108 (N = 10)	0.99/0.11	2.90/0.06	0.34/0.01
Cancellaria spengleriana: USNM 664965; USNM 344417 (N = 6)	1.08/0.07	3.02/0.09	0.36/0.02
Trigonostoma scalare: USNM 846304 (N = 1)	0.96	2.0	0.48
Olssonella smithii: USNM 806986; USNM 450577; USNM 667720 (N = 5)	0.85/0.04	2.62/0.16	0.33/0.02
Narona mitraeformis: Petit collection (N = 3)	1.06/0.03	3.60/0.15	0.29/0.00
Scalptia obliquata: USNM 629063 (N = 4)	0.89/0.03	2.45/0.09	0.36/0.01
Cancellaria similis: USNM 664967 (N = 5)	1.26/0.06	2.75/0.00	0.46/0.02

(as *Velutina undata* Brown, see Thorson, 1944); Bouchet & Warén, 1985: fig. 687]. The egg capsules of all cancellariids studied to date have roughly elliptical, parallel sides with strongly to weakly keeled margins, and a medial, dorsal hatching aperture. Capsules with very long stalks appear to be restricted to the subfamily Cancellariinae.

Development of *Cancellaria cooperi* is similar to that of *Thais haemastoma floridana* as described by D'Asaro (1966), although *C. cooperi* takes about 80% longer to reach comparable developmental stages, and does not produce a noticeable sinusigeral ridge. It is interesting to note the presence of an operculum, particularly prominent in the planktotrophic larval stage (figure 21), in a family noted for the absence of opercula in adults.

The present study comprises the first direct observation of oviposition and development of any species of cancellariid, although the mode of development can be deduced in several cases from previously published data on capsule contents. Thus, *Cancellaria* sp. (30–40 ova/capsule, 500 μm in diameter; Knudsen, 1950:109), *Trigonostoma foveolata* (16 larvae/capsule; Petit & Harasewych, in preparation), *Admete viridula* (6–7 larvae/capsule; Thorson, 1935:67) and *Admete* sp. (6 larvae/capsule, capsule referred to by MacGinitie, 1955:51, USNM 664468) all likely undergo lecithotrophic development, as indicated by the low number of large larvae or ova per capsule. To date, *Cancellaria cooperi* is the only cancellariid known to undergo planktotrophic development.

In the absence of direct information, gastropod larval development may be inferred from the morphology of the protoconch at the apex of the adult shell. Thorson's "apex theory" (Thorson, 1950; Jablonski & Lutz, 1980, 1983) asserts that a large, rounded, paucispiral protoconch indicates non-planktotrophic larval development, while a narrow, polygyrate, sculptured protoconch suggests planktotrophic development. In more quantitative studies of this relationship, Shuto (1974) found that the ratio of the maximum protoconch diameter (D) to the number of protoconch whorls (Vol) was a reasonable indicator of developmental type. Values greater than 1.0 were indicative of lecithotrophic larvae, while values below 0.3 were more characteristic of planktotrophic

larvae, especially if the protoconch consisted of three or more whorls. Species with D/Vol ratios between 0.3 and 1.0 usually have lecithotrophic larvae if protoconchs consist of less than 2¼ whorls. A plot of Vol *vs.* D/Vol values for 10 species of cancellariids (figure 23) indicates that although protoconch morphology appears to be an accurate indicator of the mode of larval development for those species of Cancellariidae that fall within the diagnostic regions proposed by Shuto (1974), developmental type cannot be inferred for the majority of cancellariid taxa using these criteria.

As more information on the life histories and diets of additional species of cancellariids becomes available, the relationship between the mode of larval development and the mobility and patchiness of prey species distribution may prove fruitful ground for investigation.

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Latirus martini (Gastropoda: Fasciolariidae), a New Species from Honduras

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ABSTRACT

Latirus martini new species is described from shallow water off Roatan Island, approximately 40 miles north of the Honduras mainland. This new taxon differs from its nearest Caribbean relative, *Latirus angulatus* (Röding, 1798), by its sculpture, coloration, shape, and size. The 13–16 axial ribs on the body whorl constitute roughly twice the number found in other Caribbean members of this genus.

INTRODUCTION

In the summer of 1985 10 specimens of a new *Latirus* were taken under coral rubble by divers off the north coast of Roatan Island, Honduras. These shells were obtained by Mr. Thomas Honker of Florida, who kindly passed them on to the author. The specimens were all collected alive, the soft parts discarded, and the opercula glued back in place on cotton. For this reason no soft parts were examined, although the operculum is described. Since that time, some additional specimens have been taken from the same locality.

Specimens of the new species are deposited in the collections of the Academy of Natural Sciences of Philadelphia (ANSP), the Delaware Museum of Natural History (DMNH), and the National Museum of Natural History, Smithsonian Institution (USNM). Additional specimens are retained in the collection of the author.

Family **Fasciolariidae** Gray, 1853
Subfamily **Peristerniinae** Tryon, 1880

Genus *Latirus* Montfort, 1810

Type species: *Latirus aurantiacus* Montfort, 1810, by monotypy [= *L. gibbulus* (Gmelin, 1791)].

Latirus martini new species
(figures 1, 2)

Description: Shell heavy, small to medium in size (21.7 mm to 38.4 mm in length), somewhat squat, with spire nearly ⅓ length of shell; profile inflated, with 8–9 whorls; protoconch (figure 2) of 1½ whorl, smooth, bulbous, translucent pale orange-brown in color; aperture oval to squarish, greater in length than siphonal canal; anal canal weakly developed; axial sculpture of 13–16 prominent ribs, crossed by numerous, pronounced spiral cords with grooves between; cords alternately larger and smaller, first two on body whorl about equal in thickness, forming ridge and deep suture; approximately 45 cords on body whorl running onto anterior end of siphonal canal, 25 cords on the penultimate whorl, with every fifth cord somewhat stronger than others; spiral cords darkish orange-brown turning to dark brown between axial ribs; grooves between cords light caramel brown with yellow cast; shell appears dark orange-brown, with lighter axial ribs; columella with 3–4 distinct plicae (figure 1); teeth translucent, shiny, white; outer lip crenulated, with indentations corresponding to spiral sculpture; smooth portion of inner lip extending approximately to opposing side of the first axial rib, followed anteriorly by 14–16 irregular white lirae on inside of body whorl; operculum yellow-brown in color, chitinous, nearly filling aperture.

Type locality: 15–20 feet, under coral rubble, north coast, Roatan Island, Honduras, summer, 1985.

Type material: Holotype, ANSP 361064 (27.5 mm); paratype 1, DMNH 169442 (23.8 mm); paratype 2, USNM 859070 (26.9 mm); paratypes 3–5 in the author's collection (34.0 mm, 24.8 mm, 23.6 mm). All paratypes from the type locality.

Etymology: The species is named for the author's eldest son.

Disenssion: This species appears to be most closely related to the highly variable *Latirus angulatus* (Röding, 1798). Several forms of the latter were illustrated by Bullock (1968, 1974). Specimens of *L. angulatus* from the Swan Islands, approximately 120 miles north of Honduras (Bullock, 1968: fig. 5, plate 2), and a specimen from the northern coast of South America (Bullock, 1974: fig. 21) are superficially similar to *L. martini*. The coloration is similar but the shape and sculpture are completely typical of *L. angulatus* and thus readily distinguishable from *L. martini*. *Latirus angulatus* has 7–9 axial ribs, about half the number of *L. martini*. The spiral cords on *L. angulatus* are weaker than those of *L. martini*. The typical coloration is also quite different. In a
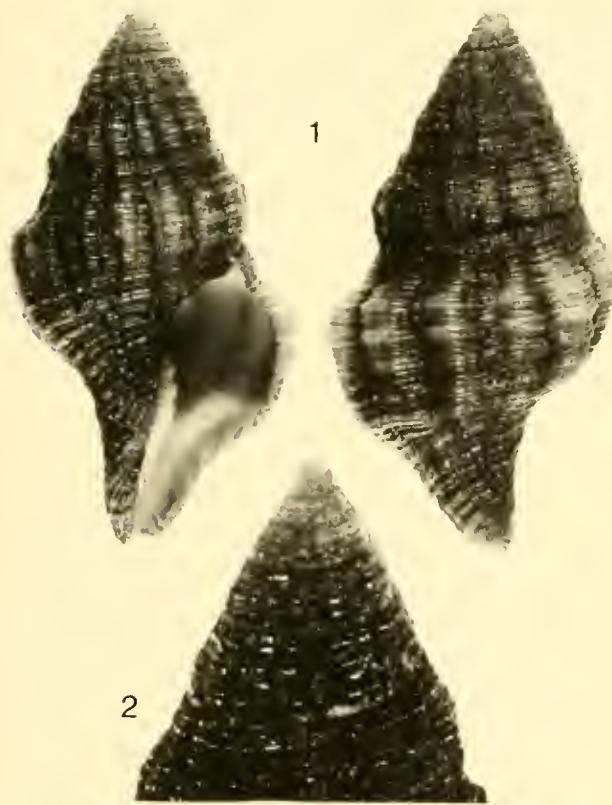
Figures 1, 2. *Latirus martini* new species. **1.** Holotype, ANSP 361064. **2.** Early whorls of paratype, DMNH 169442, both from north coast of Roatan Island, Honduras, under coral rubble in 5–7 m.

dark brown specimen of *L. angulatus*, the raised cords and that portion of the whorl near the suture are dark brown, in areas between cords where there is fine or- namentation, the shell is light cocoa-tan to orange-brown.

Generally, *L. angulatus* is a more elongated shell with the spire usually more than half the length of the shell.

Possible confusion could also occur with *Leucozonia nassa* (Gmelin, 1791) which is somewhat similar in pro- file and coloration. This shell lacks the strong axial sculp- ture of *L. martini*, and has a thick, black-brown oper- culum. A characteristic narrow white band at the base, commonly terminating in a small spine on the outer lip, serves to distinguish this species from *L. martini*.

Finally, confusion might arise with the recently-de- scribed species *Latirus vermeiji* (Petuch, 1986). *Latirus vermeiji* has less pronounced surface sculpture, is dis- tinctly orangish in color, and has a caramel-orange col- ored inner lip, whereas the inner lip in *L. martini* is yellowish brown. The roughly even spiral cords in *L. vermeiji* are more pronounced with every other cord being white in color.

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Shell Variation of Springsnail Populations in the Cuatro Cienegas Basin, Mexico: Preliminary Analysis of Limnocrene Fauna

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ABSTRACT

Geographic variation in shell morphometry is analyzed for three locally endemic springsnail (Gastropoda: Hydrobiidae) species occurring sympatrically in nine limnocrenes of the Cuatro Cienegas Basin, Coahuila, Mexico. Despite some correlation of size-related variables across species, groupings of populations based on multivariate analyses were not very similar among species, nor were they strongly concordant with current drainage configurations in the basin. Groups of populations of *Mexipyrgus churinceanus* Taylor having different patterns of shell sculpture and color banding (and once considered separate species) were not separated similarly on basis of shell size and shape. Inter-population differentiation of these snails was approximately equivalent to that of *Nymphophilus minckleyi* Taylor, whereas *Mexithauma quadripaludium* Taylor was less variable.

INTRODUCTION

One of the more remarkable aquatic faunas of the New World occurs in the small (1,200 km²), intermontane valley of Cuatro Cienegas, Coahuila, Mexico, which harbors at least 26 locally endemic forms (Cole, 1984; McCoy, 1984; Minckley, 1984; Hershler, 1985). Local aquatic taxa show a great diversity in extent of differentiation relative to adjacent biota, ranging from slightly differentiated populations to highly divergent genera, suggesting both long-term persistence of aquatic habitat and multiple invasions of the valley over a broad time scale (Minckley, 1969). Aquatic organisms are deployed among diverse, spring-fed aquatic habitats that comprise five to seven local drainage systems (Minckley, 1969; LaBounty, 1974), providing what has been termed a "matchless natural laboratory" (Taylor & Minckley 1966:22) for ecological and evolutionary study.

Springsnails (Gastropoda: Hydrobiidae) of the basin are diverse [nine genera (five endemic), 13 species (nine endemic); Hershler, 1985], and occur abundantly in a large number of easily accessible sites, providing an excellent opportunity to study geographic variation of pop-

ulations, the analysis of which is considered crucial to understanding the speciation process (Gould & Johnston, 1972; Endler, 1977). To date, research on this snail fauna has largely been taxonomic (Taylor, 1966; Hershler, 1985), although geographic variation of one endemic species was partly analyzed (Hershler, 1985; Hershler & Minckley, 1986). Taylor (1966) and Taylor and Minckley (1966) noted apparent diversity in extent of differentiation among local species: *Mexipyrgus* Taylor, an endemic restricted to large (> 25 m²) springpools (limnocrenes) and stream outflows, is variable enough to have been originally considered as six nominal species (Taylor, 1966; synonymized to monotypy by Hershler, 1985), whereas other snails appear morphologically uniform, at least in the portion of the basin that has been well studied (*i.e.*, all but the southeastern lobe; Hershler, 1985). It was suggested that heightened differentiation of *Mexipyrgus* resulted from marked discontinuity of its habitat:

> . . . it seems that habitat of this genus is more likely to be discontinuous than that of other snails in the area. *Mexipyrgus* lives in soft flocculent ooze or mud in the lagunas, thus not in the shallows where wave action removes the fine particles. Extensive marshy areas with small streams connecting larger water bodies provide no suitable widespread habitat. (Taylor, 1966:188)

Variation within *Mexipyrgus* has largely been discussed in terms of shell sculpture and color banding (Taylor, 1966), characters absent from or poorly developed in other local snails, and there has been no attempt to contrast intraspecific variation among members of the snail fauna using a set of common characters, such as shell morphometric variables. In this paper we provide such a comparison between *Mexipyrgus churinceanus* Taylor and the two other species (both local endemics) common in basin limnocrenes, *Mexithauma quadripaludium* Taylor and *Nymphophilus minckleyi* Taylor (see figure 2). Specifically, we seek to answer the following questions: 1) Do these distantly related snails (Hershler, 1985) show commonality of pattern of geographic variation? 2) Does shell morphometric variation among pop-
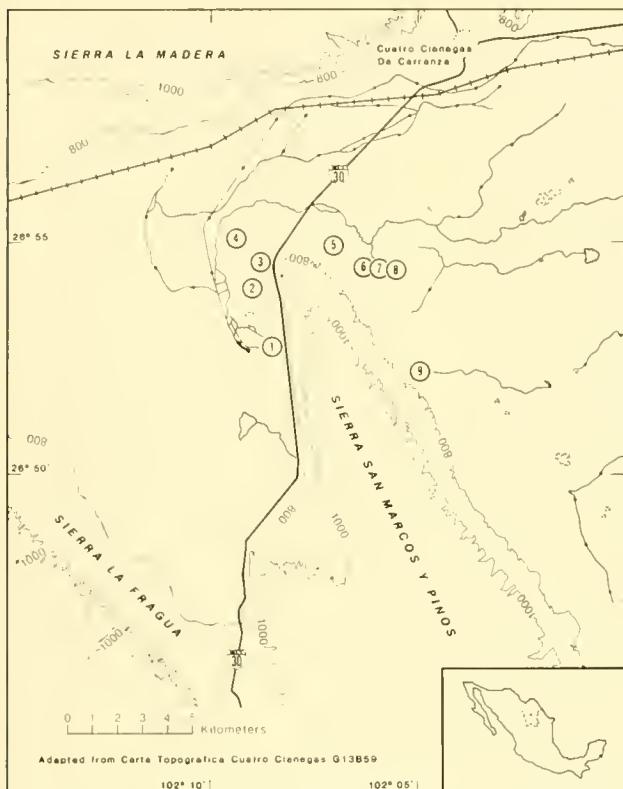
Figure 1. Map of the central portion of the Cuatro Cienegas Basin, showing major drainage features and collecting localities (numbered as in table 1). The inset (lower right) shows locations of the state of Coahuila (dashed line) and Cuatro Cienegas (dot) within Mexico.

ulations of *Mexipyrgus churinceanus* exceed that of the two other limnocrene species (above) that occur sympatrically with this species? 3) Are *Mexipyrgus* populations that are well differentiated in terms of shell sculpture and color banding patterns similarly separated by shell size and shape variation?

MATERIALS AND METHODS

Nine limnocrenes were sampled (shown in figure 1 and described in the Appendix), representing the majority of springpools in the study area (all of basin excluding southeastern lobe) where all three forms are common. Only isolated sources (Sites 1–4, 9) or, in cases where springs were connected by stream, upflow pools (Sites 5–8) were considered, in order to reduce possible effects of gene flow from contiguous populations (Hershler & Minckley, 1986). These springs belong to four separate drainage systems of the basin and harbor forms of *Mexipyrgus* referable to four nominal species (see below).

Mexipyrgus churinceanus was collected by sieving soft substrates, while the other two species, associated with hard substrates, were gathered by washing travertine and macrophytes in a bucket. Material was fixed in dilute formalin, and preserved in 70% ethanol.
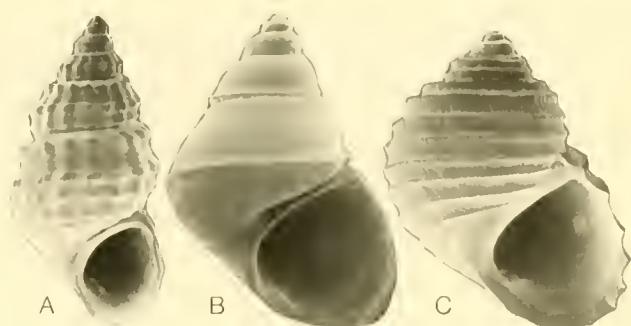
Figure 2. Scanning electron micrographs (printed at same enlargement) of cleaned shells of springsnails from Laguna Tio Candido, Cuatro Cienegas, Mexico: a, *Mexipyrgus churinceanus* (shell height, 6.34 mm); b, *Nymphophilus minckleyi* (6.45 mm); c, *Mexithauma quadripaludium* (6.22 mm).

For each species, about 15 live-collected, fully mature adults, recognizable by their complete and thickened inner shell lips, were randomly selected from collections from each site and dried for morphometric analysis. After whorls were counted (WH), shells were imbedded in clay in standard apertural aspect (figure 2) and shell outlines were drawn using a camera lucida mounted on a WILD M-5 dissecting microscope ($12\times$ or $25\times$). Points on these drawings were digitized and values for the following "standard" shell parameters (1–4) and shell shape descriptors (5–8) (from Raup, 1966, and elsewhere) were generated:

1) Shell height (SH)
2) Shell width (SW)
3) Length of body whorl (LBW)
4) Width of body whorl (WBW)
5) Translation rate (T)
6) Whorl expansion rate (W)
7) Distance of generating curve from coiling axis (D)
8) Aperture shape (SA)

A calculated variable (S), consisting of the addition of SH and SW, was generated to serve as a more realistic measure of size than either shell length or width. Calculation of shape parameters largely followed methods of Kohn and Riggs (1975), with the exception being W, which was measured as the mean of a series of squared ratios of perpendicular distances from coiling axis to sutures (shell in apertural and not apical aspect) at half whorl intervals. The apertural suture was not used, due to frequent loosening of coiling during last half whorl of growth, nor were sutures used from eroded adapical sections of the spire. Digitizing was done using the CONCH software program (Chapman *et al.*, 1988; methodology fully described therein) and a GTCO Micro-Digi Pad 12×12 linked to a KAYPRO 2000 microcomputer.

Descriptive statistics for all morphological variables were obtained for each species and locality. The hypotheses of homogeneity of mean differences and variances across localities were tested for each species. An ANOVA model was selected for each variable of each

Table 1. Descriptive statistics for each species at each locality. Data given are mean, standard deviation, and sample size (in parentheses). L = locality; variable abbreviations are given in text.

L	SH	SW	S	LBW	WBW	WH	W	D	T	SA
Mexipyrgus churinceanus										
1	5.14	2.62	7.76	3.37	2.39	6.18	1.90	0.76	6.17	1.32
(15)	0.39	0.20	0.57	0.21	0.21	0.37	0.16	0.07	0.49	0.06
2	6.13	3.21	9.34	3.85	3.00	7.03	1.81	0.67	5.87	1.36
(15)	0.30	0.11	0.35	0.19	0.12	0.57	0.19	0.04	0.53	0.06
3	4.76	2.48	7.24	2.94	2.32	6.57	1.75	0.68	6.13	1.35
(15)	0.32	0.21	0.49	0.17	0.19	0.48	0.14	0.05	0.79	0.06
4	5.02	2.72	7.74	3.44	2.47	6.23	1.97	0.73	5.99	1.35
(14)	0.23	0.12	0.29	0.16	0.12	0.27	0.16	0.06	0.27	0.07
5	3.99	2.17	6.16	2.60	2.02	6.28	1.98	0.68	6.19	1.31
(15)	0.22	0.17	0.38	0.12	0.16	0.38	0.36	0.07	0.64	0.07
6	7.30	3.98	11.3	4.68	3.55	6.55	1.86	0.61	5.77	1.36
(14)	0.56	0.33	0.84	0.24	0.36	0.41	0.21	0.04	0.67	0.04
7	6.48	3.17	9.66	4.13	2.88	7.28	2.05	0.70	6.67	1.36
(15)	0.30	0.18	0.41	0.24	0.24	0.44	0.40	0.07	0.65	0.06
8	5.49	2.54	8.03	3.57	2.24	7.03	1.92	0.73	7.13	1.41
(15)	0.18	0.14	0.25	0.14	0.09	0.61	0.28	0.06	0.87	0.06
9	7.16	3.62	10.8	4.39	3.45	6.58	1.76	0.70	6.44	1.41
(15)	0.46	0.22	0.66	0.19	0.26	0.32	0.10	0.07	0.73	0.09
Mexithauma quadripaludium										
1	7.39	6.44	13.8	6.61	4.72	4.57	2.20	0.62	3.81	1.11
(15)	0.55	0.41	0.90	0.47	0.30	0.24	0.22	0.05	0.44	0.06
2	5.82	5.07	10.9	5.09	3.64	4.47	2.26	0.60	3.14	1.13
(15)	0.41	0.28	0.66	0.42	0.24	0.23	0.32	0.04	0.40	0.06
3	5.73	4.83	10.6	5.04	3.54	4.63	2.28	0.65	3.50	1.13
(15)	0.30	0.33	0.59	0.31	0.19	0.25	0.33	0.05	0.60	0.06
4	6.20	5.45	11.7	5.45	3.99	4.37	2.05	0.62	3.52	1.07
(13)	0.57	0.36	0.87	0.58	0.25	0.26	0.21	0.06	0.60	0.08
5	5.77	5.09	10.9	5.14	3.68	4.19	2.36	0.61	3.38	1.12
(9)	0.61	0.55	1.12	0.52	0.41	0.11	0.41	0.08	0.48	0.05
6	6.72	6.00	12.7	5.76	4.51	4.44	2.07	0.61	3.34	1.03
(9)	0.60	0.49	1.07	0.47	0.47	0.41	0.11	0.05	0.48	0.05
7	5.23	4.50	9.73	4.56	3.27	4.32	2.14	0.63	2.85	1.12
(15)	0.36	0.22	0.55	0.34	0.20	0.26	0.19	0.04	0.21	0.05
8	6.07	5.15	11.2	5.18	3.78	4.67	2.20	0.62	3.17	1.10
(15)	0.48	0.30	0.72	0.42	0.25	0.29	0.25	0.07	0.37	0.06
9	6.40	5.51	11.9	5.47	4.15	4.63	2.16	0.64	3.51	1.08
(15)	0.44	0.29	0.67	0.35	0.27	0.30	0.19	0.04	0.56	0.05
Nymphophilus minckleyi										
1	6.66	5.30	12.0	5.19	4.00	4.80	2.06	0.57	3.24	1.12
(15)	0.38	0.19	0.53	0.28	0.20	0.34	0.37	0.03	0.29	0.05
2	5.99	4.56	10.6	4.51	3.76	5.03	1.88	0.59	3.82	1.09
(15)	0.47	0.31	0.73	0.34	0.22	0.09	0.19	0.05	0.43	0.03
3	5.12	4.09	9.21	3.96	3.15	4.54	2.01	0.57	3.35	1.10
(12)	0.43	0.26	0.67	0.31	0.20	0.37	0.26	0.03	0.36	0.04
4	5.88	4.89	10.8	4.50	3.79	5.39	1.89	0.54	3.32	1.05
(7)	0.39	0.15	0.42	0.25	0.09	0.35	0.12	0.02	0.33	0.04
5	5.56	4.84	9.90	4.38	3.48	5.28	2.08	0.60	3.60	1.14
(15)	0.34	0.23	0.50	0.28	0.19	0.38	0.29	0.03	0.48	0.03
6	7.17	5.98	13.1	5.29	4.84	5.68	1.86	0.54	3.19	1.13
(15)	0.30	0.26	0.45	0.24	0.18	0.26	0.16	0.04	0.42	0.05

Table 1. Continued.

					Variable					
L	SH	SW	S	LBW	WBW	WH	W	D	T	SA
7	5.69	4.53	10.2	4.13	3.74	5.22	1.76	0.58	3.45	1.07
(11)	0.29	0.27	0.54	0.19	0.26	0.14	0.04	0.05	0.24	0.05
8	7.03	5.55	12.6	5.32	4.35	5.23	1.88	0.57	3.34	1.18
(10)	0.25	0.36	0.55	0.28	0.27	0.18	0.29	0.04	0.35	0.07
9	7.48	5.85	13.3	5.61	4.61	5.47	1.83	0.59	3.21	1.17
(15)	0.46	0.30	0.68	0.35	0.30	0.27	0.13	0.06	0.32	0.06

species unless very significant heterogeneity of variance existed, in which case the generalized Welch test was used to consider mean differences. Pearson correlations were computed across species pairs for population means of each variable. Principal component analysis (PCA) was applied separately to each species data matrix to assess and compare groupings of specimens without *a priori* assumptions. Because the units of measurement were distinct and non-comparable, the analyses were performed on correlation matrices. Discriminant analysis (DA) was used to determine assignment of specimens to the locality groupings on basis of shell size and shape. This analysis was computed in a stepwise manner in order to identify measurements contributing to significance of discrimination. Selection criterion was maximization of Mahalanobis D-squared between closest pairs of localities. The *a posteriori* procedure of classification analysis was performed to determine possible error of specimen assignment to locality. When SL and SW were replaced by their sum (S), slightly better locality separation resulted in the multivariate analyses and these results are reported.

Computations were performed using SYSTAT (Wilkinson, 1986) on an IBM-XT, and SPSSX Ver. 2 on an IBM 4381 VM/CMS system at the Smithsonian Institution.

RESULTS

Descriptive summary statistics for each species by locality are in table 1. Results of locality tests for both mean differences and variance are in table 2. Heterogeneity of variance was more pronounced for *Mexipyrgus churinceanus* (significant for six variables at $P < 0.01$ level) than for the other species. Inter-locality variation was marked for each species, and in all but three cases (LBW, *Mexipyrgus churinceanus*; W, D, *Mexithauma quadripaludium*) the hypothesis of mean equality of variables across localities was rejected at 0.05 level. As an example, inter-locality variation in the size-indicator variable, S (= SH + SW), is shown in figure 3, with significant differences ($P < 0.05$) indicated by non-overlapped confidence intervals. Size range for each species is considerable; significant differences (*i.e.*, absence of overlap in figure 3) are especially numerous among populations of *Mexipyrgus churinceanus*, with overlap more

prevalent among *N. minckleyi* populations and particularly pronounced for those of *Mexithauma quadripaludium*.

For each of the three species, only three principal components were significant and yielded meaningful information. Eigenstructures show that the first component in each analysis is dominated by size and size-correlated variables (table 3), and explains 39–46% of the total variation. For *Mexipyrgus churinceanus*, two shape variables (T, SA) dominate the second component which explains almost 20% additional variability, and a sixth variable (W) is the sole measure of importance on the third axis, explaining 14%. For the other two species, size (PC1) explains 10% more variation than for *Mexipyrgus churinceanus*, whereas shape (PC2 and 3) explains only slightly less. Weights for shape parameters are spread over both the second and third axes, making interpretations of these more difficult.

Figure 4, consisting of plots of the first three PC's for each species with locality means (centroids) indicated, allows comparison of relative locations of populations in PC space among species. Spread of centroids is largely along PC1, as expected. Each plot has one or two tight clusters of a few centroids, with cluster segregation more

Table 2. Results of Analysis of Variance, or Welch's test; and Bartlett's tests for homogeneity of variance for the nine localities (**: $P < 0.01$; *: $0.01 < P \leq 0.05$; ns: $P > 0.05$).

	Variable									
	SH	SW	S	LBW	WBW	WH	W	D	T	SA
Mexipyrgus churinceanus										
Mean	**	**	**	ns	**	**	**	**	**	**
Variance	ns	*	**	*	*	ns	**	ns	*	ns
Mexithauma quadripaludium										
Mean	**	**	**	**	**	**	ns	ns	**	**
Variance	ns	ns	ns	ns	ns	ns	*	ns	*	ns
Nymphophilus minckleyi										
Mean	**	**	**	**	**	**	**	**	**	**
Variance	ns	ns	ns	ns	ns	*	**	*	ns	ns
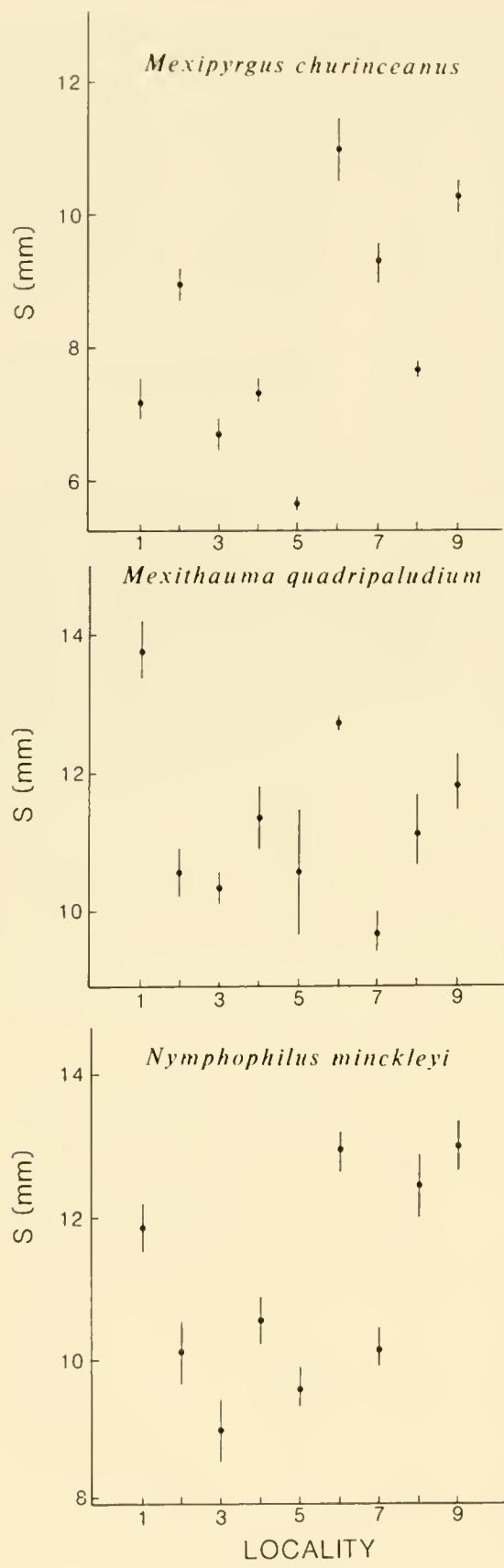
obvious for *Mexipyrgus churinceanus* and *N. minckleyi* than for *Mexithauma quadripaludium*.

Results of discriminant analyses on locality are in table 4. Size (S) is the most heavily weighted variable on DF1 for *Mexithauma quadripaludium* and *N. minckleyi*, with LBW weighting negatively; while LBW and S are approximately equally and positively weighted on this function for *Mexipyrgus churinceanus*. As with the principal components analysis, the first discriminant axis explained almost 10% more variation for *Mexipyrgus churinceanus* than for the other two species. Note that the shape parameters W and D were not correlated with any of the functions for any of the species.

Entry of the first variable (S) alone for *Mexipyrgus churinceanus* yielded significant ($P < 0.01$) separation of mean values for all but a single locality pair (1, 4). While entry of four additional variables significantly separated this final pair ($P < 0.05$), the significance level decreased to 0.082 after addition of all remaining variables. Entry of the first variable for *Mexithauma quadripaludium* (WBW) and *N. minckleyi* (S) resulted in significant separation of all but eight and five pairs, respectively; further addition of remaining variables left four and one pairs still unseparated.

Classification error rates for individual specimens indicated considerable overlap of populations, and varied across localities as follows: *Mexipyrgus churinceanus*, 53–100% correct classification [87% (overall)]; *Mexithauma quadripaludium*. 40–87% [62% (overall)]; *N. minckleyi*, 60–100% [84% (overall)]. *Mexithauma quadripaludium* was the poorest classified overall, with less than 60% classification in five of nine localities. Only three discriminant functions were significant for this species ($P < 0.05$), compared to six for the other two. Additional analyses using only shape parameters yielded considerably poorer classification [ranging from 26–39% (overall) for each species], and confirmed the low discriminating power of these variables (see Hershler & Sada, 1987).

Differentiation among drainage systems was also examined. The study area encompasses four local drainages (as recognized by LaBounty, 1974, with localities allocated to these as follows (following notes in Appendix): Becerra System (Locality 1); El Garabatal (2–4); Rio Mesquites System (5–8); and Tio Candido System (9). Clustering of populations in PC-space (figure 4) does not closely follow partitioning of localities into drainages, as indicated by considerable spread of centroids representing localities from El Garabatal (2–4), and from the interconnected springs at Los Remojos (6–8).

For further analysis, localities were re-grouped into drainage systems. A discriminant analysis on each species

Figure 3. Plots of S (SH + SW) *vs.* locality for each species. Filled circles represent medians; and bars denote simultaneous confidence intervals around the median, constructed so that if parentheses do not overlap, population medians are different at 95% confidence level.

Table 3. Results of Principal Components Analyses on each species. Only factor coefficients having weights > 0.25 are listed. I = *Mexipyrgus churinceanus*; II = *Mexithauma quadripaludium*; III = *Nymphophilus minckleyi*; Eig. = eigenvalue; % V. = % of variance explained.

	I			II			III		
	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
S	0.30			0.30			0.28		
LBW	0.30			0.30			0.27		
WBW	0.29			0.30			0.27		
T		0.55						0.44	−0.45
SA		0.44			0.43	0.59		0.36	0.31
W			−0.77		0.55				0.69
D					0.43	−0.64		0.60	
WH					−0.32	−0.37			−0.32
Eig.	3.22	1.51	1.10	3.19	1.22	1.00	3.49	1.35	1.11
% V.	39.2	19.8	13.8	45.5	17.4	14.4	45.6	16.9	13.9

using all variables was able to separate the four drainage groups only for *Mexipyrgus churinceanus*; only two functions were significant for the other species. Results of these analyses are in table 5. Note the low weights of S on DF1 for *Mexithauma quadripaludium* and *N. minckleyi* compared to these for *Mexipyrgus churinceanus*, and the relatively small amount (*ca.* 40%) of variation explained by the first function for all three species. Classification error rates for individual specimens were similar for the three species: *Mexipyrgus churinceanus*, 61–93% [68% (overall)]; *Mexithauma quadripaludium*, 46–93% [60% (overall)]; *N. minckleyi*, 57–100% [77% (overall)], with highest classification for Drainage 1 (87–100%) and lowest for Drainage 3 (46–61%).

There is similarity of pattern of size variation for the three species: populations having large-sized shells are concentrated in the southeastern portion of the study area (figure 3, Localities 6–9). For standard shell measurements, population means were significantly correlated for *Mexipyrgus churinceanus* and *Nymphophilus minckleyi* (*r* > 0.61, *P* < 0.05 for S, SL, SW, WBW) and *Mexithauma quadripaludium* with *Nymphophilus minckleyi* (*r* > 0.60, *P* < 0.05 for S, SL, SW, WBW, LBW). There were no significant correlations between *Mexipyrgus churineeanus* and *Mexithauma quadripaludium*. Population means for whorl number and shape parameters were not correlated across species with one exception (*Mexithauma quadripaludium* with *Nymphophilus minckleyi*, *r* = 0.64, *P* < 0.05 for W).

Table 4. Results of Discriminant Analyses on locality for each species. Standardized function coefficients (> 0.25) and pooled within group correlation coefficients (> 0.25) of each function with each original variable are listed. I = *Mexipyrgus churinceanus*; II = *Mexithauma quadripaludium*; III = *Nymphophilus minckleyi*; Eig. = eigenvalue; % V. = % of variance explained; C.C. = canonical correlation.
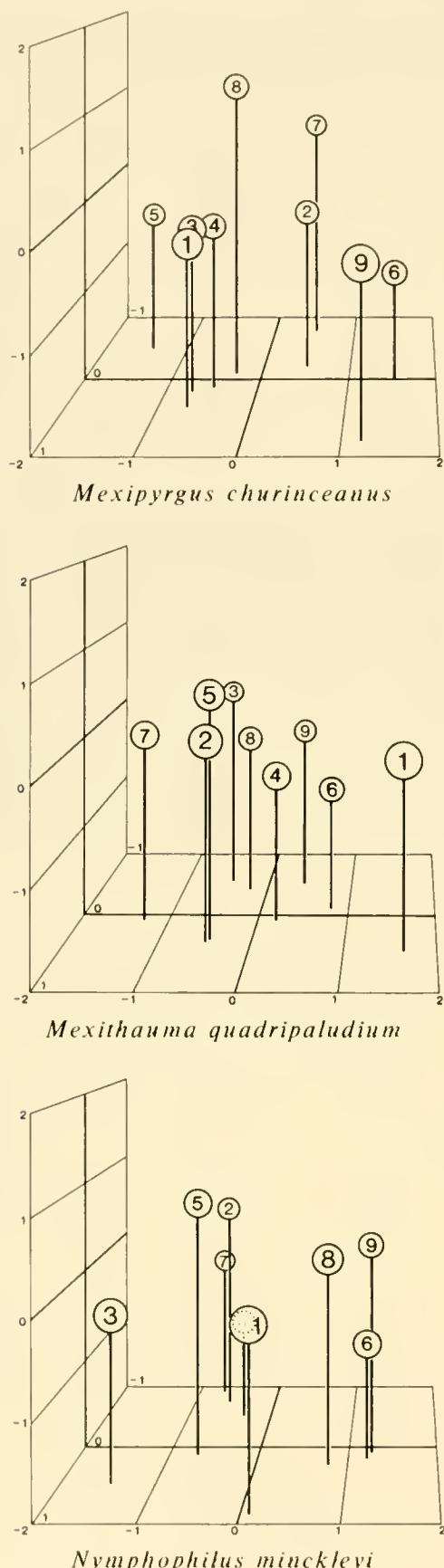
	I			II			III		
	DF1	DF2	DF3	DF1	DF2	DF3	DF1	DF2	DF3
				Standardized coefficients					
S	0.64		0.89	0.94	−0.66		1.51		−1.61
LBW	0.69	0.90	−0.95	−0.56	1.88	2.02	−1.09	−1.43	1.63
WBW	−0.35	−1.13		0.56	−0.94	−2.15	0.35	0.91	
D									
T			0.39			0.65		0.30	
SA							0.34		
WH		0.49	0.61			0.79		0.48	0.77
Eig.	13.3	2.19	0.61	3.13	0.56	0.45	8.95	2.61	0.56
% V.	79.2	13.0	3.6	70.9	12.7	10.1	69.3	20.2	4.3
C.C.	0.96	0.83	0.62	0.87	0.60	0.56	0.95	0.85	0.60
				Correlation coefficients					
S	0.89	−0.38		0.88	0.31		0.84	−0.36	
LBW	0.94			0.74	0.54		0.61	−0.53	0.38
WBW	0.64	−0.65		0.93			0.83		
T		0.34	0.31						
SA					0.46				0.34
WH			0.72			0.77	0.30	0.38	0.78

Mexipyrgus churinceanus

Mexithauma quadripaludium

Nymphophilus minckleyi

Despite these correlations, concordance of pattern among plots of PC scores for the three species is not impressive, although there is similarity in order along size-related PC1 (figure 4). Note that the tightest clustered centroids for *Mexipyrgus churinceanus* (Localities 1, 3, 4) are widely separated for the other two species. Similarly, divergent "outlying" centroids for given species (*Mexithauma quadripaludium*, 1; *N. minckleyi*, 3) are not so differentiated in the other species.

As mentioned above, the populations of *Mexipyrgus* considered in this study are referable to four nominal species (*fide* Taylor, 1966) on basis of shell sculpture and color banding: *Mexipyrgus churinceanus* (Localities 1, 2, 4); *Mexipyrgus mojarralis* (5); *Mexipyrgus lugoi* (6–8); and *Mexipyrgus carranzae* (9) (the form present at Locality 3 is distinctive and not clearly referable to any nominal species). These nominal species are poorly segregated on the PC axes: extent of separation of *mojarralis* (5) and *carranzae* (9) from other centroids, for instance, is exceeded by that seen among three populations referable to *churinceanus* in Los Remojos spring complex (6–8).

DISCUSSION

For all three species, most inter-population variation involved shell size and size-correlated variables. Commonality of geographic variation patterns was indicated by significant correlation of population means for some of these variables across two of three species pairs. The extent of this commonality was not, however, impressive when groupings of populations based on multivariate analyses were examined.

A strong correlation between geographic variation patterns and current drainage configurations was not apparent for any of the species, suggesting that in this example development of intraspecific diversity of shell morphometry may be related to ecological as well as historical factors (see Chernoff, 1982, for general discussion of this subject), although we acknowledge the possibility that the poor correlation with current drainage configuration may be obscured by historically complex basin hydrography (Minckley, 1969; Hershler & Minckley, 1985). Springpools concentrated around the northern tip of Sierra de San Marcos (where the study area is located) are highly uniform in water quality (Minckley & Cole, 1968): single measurements taken by us during the study indicated, for instance, that temperature and conductivity ranged among the nine springpools from 25.5–34.5 °C (seven localities differing by < 4 °C) and 1,825–3,500 micromhos/cm (seven localities differing by < 430 micromhos/cm), respectively. Pools do differ con-

←

Figure 4. Three-dimensional plots of PC centroids for the three species (X axis, PC1; Y, PC2; Z, PC3), standardized and viewed in perspective. Sizes of balls indicating centroids are scaled to heighten perspective.

Table 5. Results of four-group Discriminant Analyses on drainage system for each species. Standardized function coefficients (> 0.25) and pooled within group correlation coefficients (> 0.25) of each function with each original variable are listed. I = *Mexipyrgus churinceanus*; II = *Mexithauma quadripaludium*; III = *Nymphophilus minckleyi*; Eig. = eigenvalue; % V. = % of variance explained; C.C. = canonical correlation.

	I			II			III		
	DF1	DF2	DF3	DF1	DF2	DF3	DF1	DF2	DF3
Standardized coefficients									
S	2.28	0.72	2.39	−0.49	2.11	0.84	0.87	1.76	−2.78
LBW	−2.53	0.71		1.43	−3.12	−0.46	1.41	−1.49	1.35
WBW	1.05	−0.98	−1.87		1.23	−0.91	−1.50		1.71
W									0.61
D	0.52	−0.46	0.66		0.57				−0.67
T		0.55				0.87			
SA	0.38				0.42			0.67	
WH	−0.36		−0.63			0.51		0.53	
Eig.	3.21	1.51	1.10	3.24	1.26	1.03	3.49	1.35	1.11
% V.	40.2	18.8	13.8	40.4	15.8	12.9	43.6	16.9	13.9
C.C.	0.642	0.499	0.431	0.710	0.426	0.262	0.744	0.717	0.217
Correlation coefficients									
S	0.58	0.35		0.89	0.32		0.49	0.63	
LBW	0.48	0.58		0.96			0.61	0.57	
WBW	0.65	0.36		0.80	0.50		0.83		
W									0.61
D		−0.36	0.59						−0.50
T		0.47		0.40		0.68			−0.33
SA	0.31				−0.32			0.46	
WH		0.44	−0.47		0.31	0.48		0.68	

siderably in other potentially important parameters such as size, substrate composition, and abundance of molluscivorous cichlid fishes and the relationship between these features and shell geographic variation merits further study.

Groupings of populations of *Mexipyrgus churinceanus* on basis of shell size and shape were not strongly concordant with allocation of these to nominal species defined by shell color banding pattern differences. Furthermore, both univariate and multivariate analyses showed that these populations were no more differentiated in terms of shell size and shape than were those of seemingly monomorphic *Nymphophilus minckleyi*. These results suggest that evolution within *Mexipyrgus* has been mosaic, with development of striking diversity in shell color banding patterns and a few other features (including aspects of shell sculpture, and penial lobation pattern) coupled with unremarkable divergence in shell morphology.

It is intriguing that these snails and *N. minckleyi*, which differ greatly in microhabitat and presumed potential for gene flow between populations at spring sources, have similar levels of intraspecific shell morphometric divergence, whereas *Mexithauma quadripaludium*, which broadly overlaps in niche with the latter (Hershler, 1984), is less variable. The possibility that these patterns reflect differing times of origin of lineages within the basin is not currently testable due to absence of fossil evidence.

ACKNOWLEDGEMENTS

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APPENDIX

Springpools sampled are numbered as in figure 1. Locality names are either those of Minckley (1969) or reflect local usage. Locality data represent air distances from Cuatro Cienegas. Dates of collection are given in parentheses. Catalog numbers (USNM) for voucher material (dry shell plus alcohol specimens) from each locality are given in following order: *Nymphophilus minckleyi* Taylor, *Mexipyrgus churinceanus* Taylor, and *Mexithauma quadripaludium* Taylor.

1. Poso de la Becerra [(south pool) 3-IX-86], 13.7 km W-SW of Cuatro Cienegas. A once enormous spring area (over a kilometer long) significantly reduced in size by canal development in early 1960's (see Taylor, 1966:162; Minckley 1969: figs. 15, 16). Currently consisting of two large springpools (each *ca.* 50 × 125 m²) connected by short section of stream. Spring orifices few and large, occurring in deepest (to 7 m) portion of pools. Water lily stands extensive. Spring and outflow constituting a major

drainage of basin now feeding canals. USNM 857909, 857918, 857927.

Sites 2–4 represent three springs in the area known as El Garabatal, located north of Poso de la Becerra and east of Becerra's outflow. El Garabatal drains to the north and west, and may be considered either a separate, small drainage or a subset of the Rio Mesquites system, the largest drainage in the basin.

2. Lagunas de Juan Santos (5-IX-86), 12.8 km W-SW of Cuatro Cienegas. Largest of El Garabatal springs consisting of series of relatively shallow (depths to 2.0 m), inter-connected lagunas fed by springs emerging along pool margins. Pool area somewhat larger than that of Poso de la Becerra. Extensive marshes bordering near-entirety of spring's perimeter. Water lily stands extensive. Stream outflow extending several hundred meters before terminating in shallow marshy area. USNM 857912, 857921, 857930.

3. Unnamed small spring, known to biologists working in area as North Spring (3-IX-86), 12.0 km W-SW of Cuatro Cienegas. Small springpool *ca.* 12 × 18 m, about a meter deep, with *ca.* 20% coverage by water lily. Outflow entering second pool (not a spring); discharge from latter extending 50 m before disappearing into hole. USNM 857910, 857919, 857928.

4. Unnamed large spring (5-IX-86), 11.8 km W-SW of Cuatro Cienegas. Roughly circular springpool, *ca.* 70 m across; depths not exceeding 3.5 m. Water lily dense in center of pool. Outflow feeding small marsh. USNM 857916, 857925, 857934.

5. "West" Laguna in El Mojarral (4-IV-86), 9.0 km SW of Cuatro Cienegas. Moderate-sized spring (26 × 59 m; Arnold, 1972:12), with depths to 4.5 m. Orifices few in number, cavernous. Water lily stands few, relatively thin. Water exiting spring via both a shallow, surficial stream and single, tubular, subsurface vent. Stream outflow entering "East" Laguna, which in turn drains into Rio Mesquites. USNM 857908, 857917, 857926.

Sites 6–8 are inter-connected springpools known locally as Los Remojos, 9.0 km S-SW of Cuatro Cienegas. Site 6 drains into a large pool receiving discharge from a second pool fed by outflows from Sites 7 and 8. System draining into Rio Mesquites.

6. Northernmost of Los Remojos springs (5-IX-86). Pool *ca.* 18 × 32 m. Depths generally > 1.5 m; water lily common. USNM 857913, 857922, 857931.

7. Intermediate Los Remojos spring (5-IX-86). Pool *ca.* 28 × 47 m, shallow (< 1.0 m). Water lily uncommon. USNM 857914, 857923, 857932.

8. Southernmost of Los Remojos springs (5-IX-86). Pool moderately large (22 × 42 m), with depths increasing in southern end of pool to 4.0 m. Water lily common. USNM 857915, 857924, 857933.

9. Laguna Tio Candido (5-IX-86), 12.5 km S-SW of Cuatro Cienegas. Large spring (*ca.* 45 × 100 m) extensively vegetated by water lily and other macrophytes. Depths generally from 2.0–4.0 m. Outflow extending eastward, comprising part of a major system positioned south of Rio Mesquites drainage. USNM 857911, 857920, 857929.

Niche Congruency of Freshwater Gastropods in Central North America with Respect to Six Water Chemistry Parameters

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ABSTRACT

Occurrences of freshwater gastropods were studied at 430 sites in central North America with respect to total alkalinity, total dissolved solids, chloride, sulphate, phosphorus, and dissolved organic matter. Mean niche positions for the gastropods were calculated for the six combined water chemistry parameters by comparing mean values for each species using agglomerative hierarchical cluster analysis. Total niche relations were examined by calculating and summing the amount of overlap in the observed ecological tolerance ranges for the six parameters for each species pair, and applying cluster and principal component analyses. The results showed that the species occupied a broad spectrum of niches, with progressively increasing ecological range. Gastropods with low mean inorganic values and narrow niche widths were interpreted as specialists for waters with low concentrations of dissolved inorganic materials. Species which clustered together in terms of central tendencies of occurrence often differed from each other in terms of overall niche similarity, and vice versa. Competition may have been more important in waters with low inorganic concentrations.

INTRODUCTION

A number of workers have demonstrated the importance of water chemistry in the distribution of freshwater gastropods (*e.g.*, Boycott, 1936; Hubendick, 1947; Aho, 1966; Harman & Berg, 1971; Dussart, 1976; Pip, 1978, 1985, 1986; Okland, 1979; Okland & Okland, 1980). However, aside from the pioneering study of Finnish lakes by Aho *et al.* (1981), relatively little is known regarding niche relationships between freshwater gastropod species that coexist within a given geographical area.

The ecological niche of a species can be described as an infinite hyperspace representing all physical and biotic aspects of the environment in which the species occurs. Nevertheless, practical considerations restrict most niche studies to a few selected parameters that are thought to be important for the species (Levins, 1968 in Aho *et al.*, 1981). According to the latter worker, the niche of a species with respect to a given parameter can be approximated by observing the species distribution over a range of values of the parameter in a number of environments.

The objective of the present study was to examine niche relationships for the freshwater gastropods in central North America in six water chemistry dimensions: total alkalinity, total dissolved solids, chloride, sulphate, molybdenum reactive phosphorus, and dissolved organic matter (DOM). These factors were chosen because a previous study (Pip, 1987) showed that these variables contribute towards variation in species richness of freshwater gastropod communities within the study area. In the present study a niche was defined as the range between the minimum and maximum values observed for each species in the study area, and was thus analogous to the concept of the "realized niche" discussed by Hutchinson (1957).

MATERIALS AND METHODS

A total of 430 sites was examined in central North America (47°–54°N and 94°–106°W) during the May–September, 1972–85 seasons. All sites contained water year-round. Ponds (< 10 ha) comprised 41.0% of the sites sampled, lakes (> 10 ha) 41.5%, rivers (> 2 m deep) 10.3%, and creeks (< 2 m deep) 7.2%. Each site was examined for snails by wading or canoeing; snails on macrophytes were obtained by dredging with a rake or by using SCUBA. Search time at each site was limited to 1 hr.

Surface water samples were collected at most sites, but at depths of >3 m where macrophytes did not reach the surface a van Dorn sampler was used. The samples were placed on ice in darkness and frozen within a maximum of 48 hr. Samples were analyzed using methods recommended by the American Public Health Association (1971).

While most of the sites were sampled only once, approximately 50 of the locations were resampled at different times of the growing season and in different years. For such sites, extreme low and high water chemistry values were used for statistical analyses. Because of environmental heterogeneity, large lakes were sampled at different locations which were treated as separate sites.

Mean and niche comparisons were made using agglomerative hierarchical cluster analysis (Sneath & Sokal,

1973). Ward's method, a minimum variance technique (Wishart, 1969) was used for clustering. Cluster fusion distances were calculated by means of the squared Euclidean distance measure:

$$\text{Distance}_{x,y} = \Sigma_i\,(x_i - y_i)^2$$

Because Ward's method is an intensely clustering procedure, ranking of the species in the dendrograms was checked for misclassifications by comparing with the ranking obtained using the unweighted pair-group method (Clifford & Stephenson, 1975), a weakly clustering strategy (Sneath & Sokal, 1973). The two methods showed similar relative ranking; thus misclassifications were not apparent. Since the relative importance of the six parameters differed with species and situation (Pip, 1987), all parameters were weighted equally in the cluster analyses.

In construction of the dendrogram for mean niche position (figure 1), mean values for each of the six parameters were used to construct a data matrix for the comparison of taxa with respect to the mean positions of their niches. Because of differences in units and statistical distributions of the six chemical parameters, values were converted to standardized Z scores, each parameter with a mean of 0 and a standard deviation of 1. Ward's method was applied to the Z scores.

The first step in niche comparison was the construction of a combined niche congruency matrix for the six chemical parameters. For each parameter, the amount of overlap in the observed ecological ranges of each species pair was divided by the combined range of the two species (range between lowest minimum and highest maximum values). Parameter values were not standardized. The six overlap proportions were then summed for each species pair (maximum possible value 6.0). The combined coefficients formed a niche congruency matrix that was analyzed using cluster analysis as above to give the dendrogram in figure 2.

The niche congruency matrix was also examined using principal component analysis (Tatsuoka, 1971), based on the error correlation matrix. Components were orthogonally rotated so that the first principal component lay along the direction of greatest variance.

Statistical programs used for dendrogram construction and principal component analysis were obtained from SPSS, Inc., Chicago, Illinois.

RESULTS

The ranges of concentrations of the inorganic chemical parameters encompassed at the study sites have been presented elsewhere (Pip, 1986). The inorganic parameters showed a number of significant ($P < 0.05$) positive intercorrelations at the study sites (table 1) and could therefore be regarded as a block with many similar trends. However DOM was significantly correlated only with molybdenum reactive phosphorus and total dissolved solids.

Five or more sets of water chemistry data were available for 36 species in the present study (table 2); only these species were included in cluster and principal component analyses. The bulk of the mean, maximum, and minimum values on which analyses were based are given by Pip (1986) for all parameters except DOM, which is given in table 2.

The dendrogram for mean niche positions (figure 1) with respect to the six combined parameters reflected the locations in the ecological ranges where each species was most often found. Cluster 1 consisted of species with the lowest mean values for total dissolved solids and low values for all other inorganic parameters. On the other hand, *Armiger crista*, *Physa jennessi*, and *Fossaria modicella* differed the most from all other species; these gastropods showed the highest mean values for total dissolved solids, as well as high values for all other parameters (Pip, 1986), including DOM. Other species in the spectrum could show low or high values of DOM which were largely unrelated to the concentrations of inorganic parameters; for example *Valvata tricarinata*, *Fossaria decampi*, and *Stagnicola catascopium* showed the lowest mean values for DOM of all species except *Campeloma decisum* (table 2).

The relations between species in terms of niche congruency for the six parameters are represented by the dendrogram in figure 2. The groups that emerged formed a spectrum of the ranges of chemical environments in which each species was observed. Clusters 1 and 2 consisted of species that showed narrow tolerance ranges for

Table 1. Correlations between water chemistry parameters at the study sites. Upper diagonal = r, lower diagonal = p. N = 446–468.

	Total dissolved solids	Total alkalinity	Chloride	Sulphate	Molybdenum reactive phosphorus	Dissolved organic matter
Total dissolved solids	X	0.47*	0.66*	0.61*	0.26*	0.10*
Total alkalinity	<0.001	X	0.39*	0.15*	0.41*	0.07
Chloride	<0.001	<0.001	X	0.61*	0.05	0.04
Sulphate	<0.001	0.001	<0.001	X	0.05	0.04
Molybdenum reactive phosphorus	<0.001	<0.001	0.14	0.14	X	0.13*
Dissolved organic matter	0.017	0.08	0.22	0.22	0.004	X

* Significant correlation.

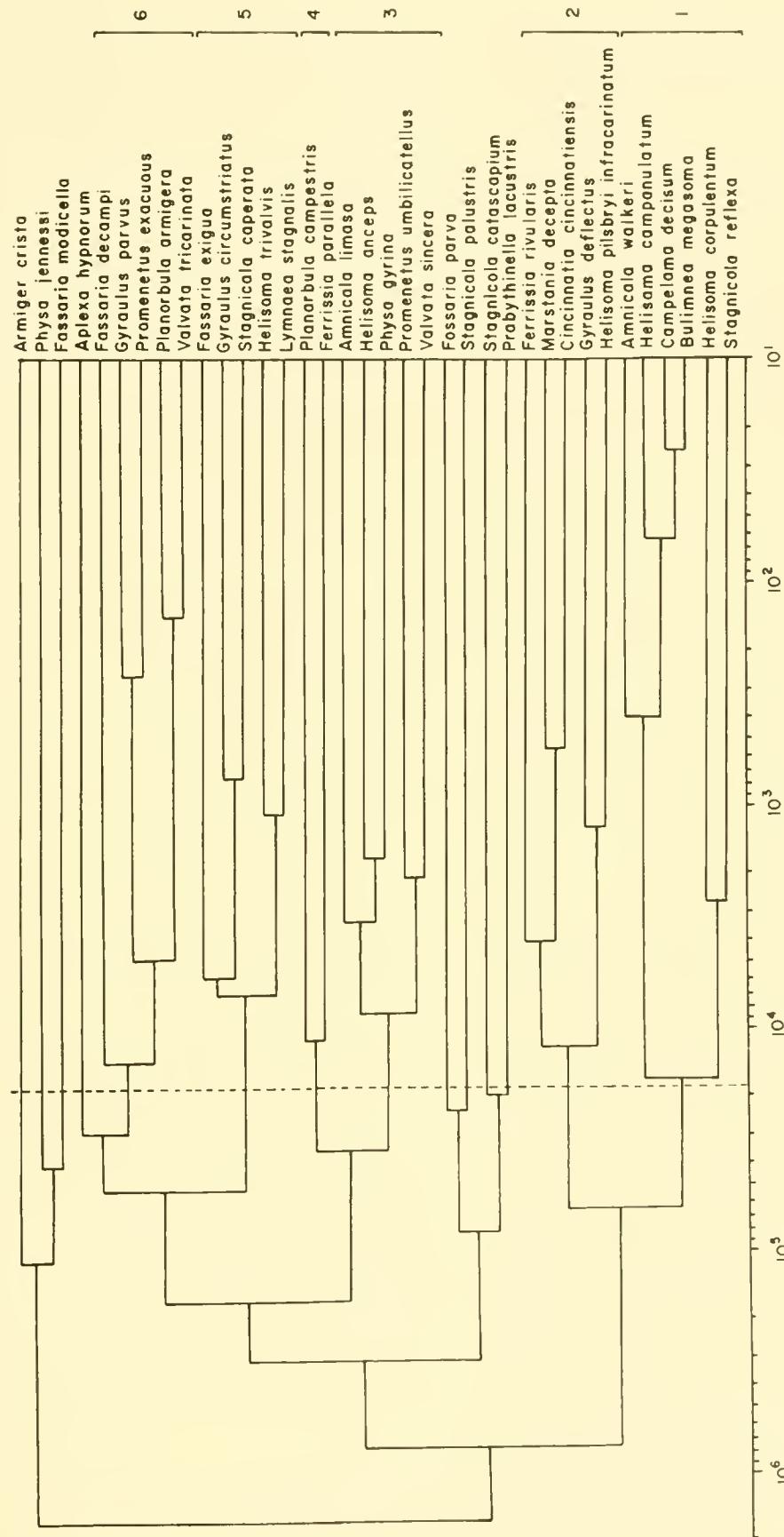**Figure 1.** Dendrogram of gastropods clustered with respect to mean niche position for the six water chemistry parameters. Scale is logarithmic. Cluster boundaries are indicated by the dashed line.
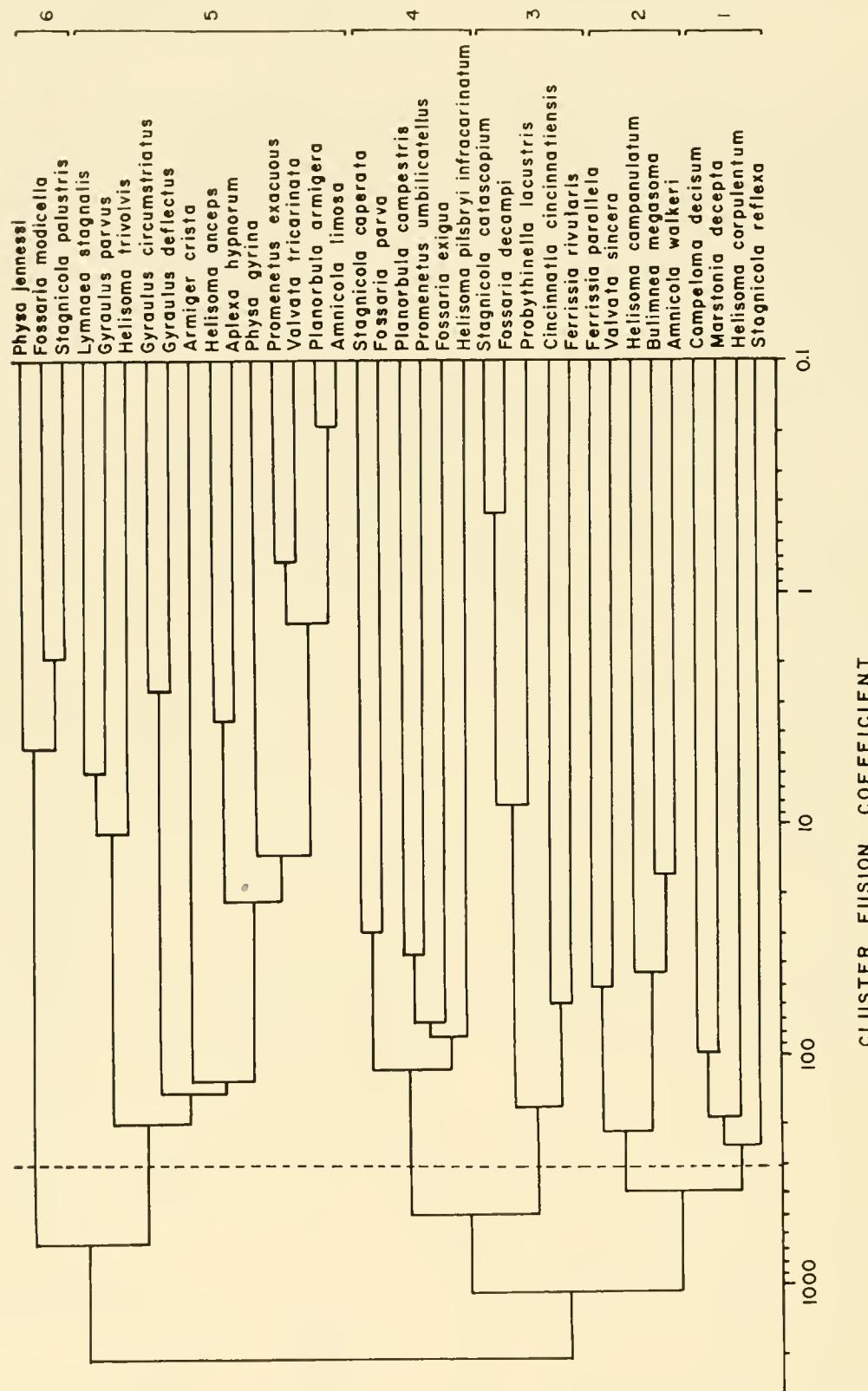
Figure 2. Dendrogram showing niche congruencies for the gastropods in the study area with respect to the six water chemistry parameters. Scale is logarithmic. Cluster boundaries are indicated by the dashed line.

the inorganic parameters at low concentrations (Pip, 1986). The narrow tolerance ranges of these species contributed towards larger interspecific differences, as seen from the larger cluster fusion coefficients; niche overlap with species that had broad ranges was small, while the probability that significant proportions of the niches of any two species with restricted ranges would not coincide was increased by the narrowness of the respective ranges. As a result, relative niche differentiation was better defined in waters with low inorganic concentrations.

Species with broader ecological tolerance ranges, on the other hand, could occur in waters with high inorganic concentrations, although in most cases they could also tolerate comparatively low values. These species formed the clusters on the upper part of the dendrogram in figure 2, and were more numerous than species which were restricted to a narrow range of environments. The greater similarity between members of each of these clusters derived from the larger degree of overlap that necessarily arose as a result of the broad ranges. Cluster 6, composed of *Stagnicola palustris*, *Fossaria modicella*, and *Physa jennessi*, represents species that occurred in the broadest range of chemical environments.

Niche relations were also examined using principal component analysis applied to the niche congruency error matrix, which extracted two major components that accounted for 55.4% and 22.7% of the variance, respectively. The remaining components each accounted for 5% or less of the remaining variance. The niche relations for individual species are plotted with respect to the first two principal components in figure 3. The distributions that emerged reflected the groupings of figure 2, although clusters 1 and 2 from figure 2 showed close affinities (groups A and B) in figure 3. Species in groups A and B showed narrow niche widths and low mean parameter values. Species in groups E and particularly F showed wide ecological ranges; these groups also included the most common species in the study area (Pip, 1978).

The first principal component of the niche congruency error matrix was significantly correlated with mean values for the respective species of all six parameters (total alkalinity $r = 0.49$, $P = 0.001$; total dissolved solids, phosphorus, and chloride, all $r = 0.47$, $P = 0.002$; sulphate $r = 0.36$, $P = 0.016$; DOM $r = 0.33$, $P = 0.023$; all $N = 36$). This large number of correlations derived from intercorrelations of these parameters at the sites examined (table 1). The strong correlations with the first component are interesting, in that the values in the original congruency matrix were not themselves correlated with any of the chemical parameters. The second principal component showed no significant correlations with the mean values of the parameters examined and was apparently related to an unmonitored factor.

DISCUSSION

Cluster analysis showed that the gastropods within the study area occupied a broad spectrum of chemical niches.

Table 2. Mean, maximum, and minimum values of dissolved organic matter (absorbance of acidified water at 275 nm) observed for the gastropods in the study area.

Species	$\bar{x}$	Minimum	Maximum	N
Campeloma decisum (Say, 1816)	0.142	0.060	0.200	6
Valvata sincera Say, 1824	0.313	0.106	0.737	7
V. tricarinata (Say, 1817)	0.204	0.018	1.366	70
Cincinnatia cincinnatiensis (Anthony, 1840)	0.210	0.054	1.366	42
Marstonia decepta (Baker, 1928)	0.209	0.053	0.665	8
Probythinella lacustris (Baker, 1928)	0.299	0.180	0.387	8
Amnicola limosa (Say, 1817)	0.263	0.039	1.428	102
A. walkeri Pilsbry, 1898	0.212	0.054	0.815	23
Lymnaea stagnalis Linne, 1758	0.325	0.018	1.676	285
Bulimnea megasoma (Say, 1824)	0.356	0.054	1.383	45
Stagnicola palustris Muller, 1774	0.314	0.060	1.638	182
S. catascopium (Say, 1817)	0.169	0.053	0.395	13
S. caperata (Say, 1829)	0.349	0.252	0.438	6
S. reflexa (Say, 1821)	0.311	0.130	1.089	7
Fossaria decampi (Streng, 1896)	0.167	0.060	0.366	9
F. exigua (Lea, 1841)	0.266	0.030	0.817	15
F. modicella (Say, 1825)	0.345	0.039	1.400	53
F. parva (Lea, 1841)	0.244	0.095	0.392	6
Physa gyrina Say, 1821	0.307	0.009	1.638	293
P. jennessi skinneri Taylor, 1953	0.387	0.042	1.306	33
Aplexa hypnorum (Linne, 1748)	0.442	0.053	1.638	41
Ferrissia parallela (Haldeman, 1841)	0.426	0.115	0.815	6
F. rivularis (Say, 1817)	0.315	0.054	1.168	53
Helisoma trivolvis (Say, 1816)	0.341	0.018	1.968	207
H. pilsbryi infracarinatum Baker, 1932	0.254	0.050	0.684	23
H. corpulentum (Say, 1824)	0.214	0.173	0.263	5
H. campanulatum (Say, 1821)	0.237	0.009	0.817	109
H. anceps (Menke, 1830)	0.280	0.009	1.512	122
Planorbula armigera (Say, 1821)	0.435	0.088	1.638	73
P. campestris (Dawson, 1875)	0.385	0.140	0.650	7
Promenetus exacuous (Say, 1821)	0.324	0.053	1.428	84
P. umbilicatellus (Cockerell, 1887)	0.240	0.053	0.625	7
Armiger crista (Linne, 1758)	0.483	0.364	0.815	17
Gyraulus parvus (Say, 1817)	0.345	0.030	1.676	193
G. circumstriatus (Tryon, 1866)	0.347	0.053	1.428	27
G. deflectus (Say, 1824)	0.273	0.054	1.428	70

In general, the species groupings in terms of niche similarity formed a continuous series with progressively greater ecological range. The niches of most species overlapped to some extent, and only a few were mutually
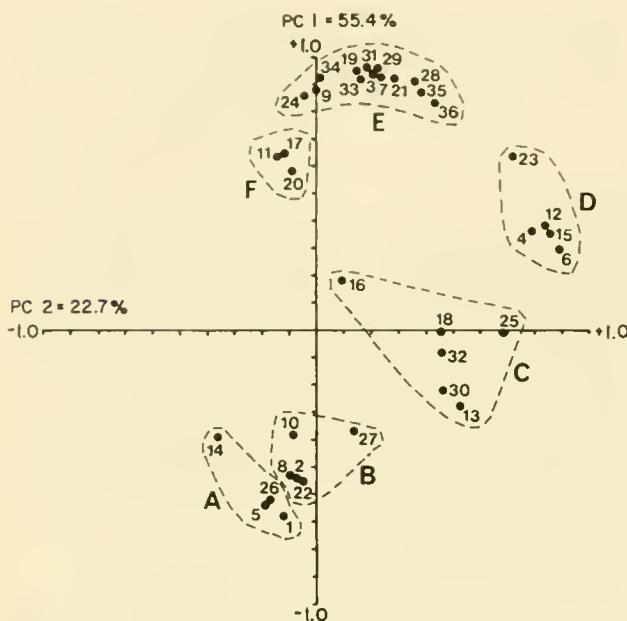
Figure 3. Distribution of species plotted with respect to the first two principal components of the niche congruency error matrix. Axes have been orthogonally rotated. Numbers represent the following species: 1—*Campeloma decisum*, 2—*Valvata sincera*, 3—*V. tricarinata*, 4—*Cincinnatia cincinnatiensis*, 5—*Marstonia decepta*, 6—*Probythinella lacustris*, 7—*Amnicola limosa*, 8—*A. walkeri*, 9—*Lymnaea stagnalis*, 10—*Bulimnea megasoma*, 11—*Stagnicola palustris*, 12—*S. catascopium*, 13—*S. caperata*, 14—*S. reflexa*, 15—*Fossaria decampi*, 16—*F. exigua*, 17—*F. modicella*, 18—*F. parva*, 19—*Physa gyrina*, 20—*P. jennessi*, 21—*Aplexa hypnorum*, 22—*Ferrissia parallela*, 23—*F. rivularis*, 24—*Helisoma trivolvis*, 25—*H. pilsbryi infracarinatum*, 26—*H. corpulentum*, 27—*H. campanulatum*, 28—*H. anceps*, 29—*Planorbula armigera*, 30—*P. campestris*, 31—*Promenetus exacuous*, 32—*P. umbilicatellus*, 33—*Armiger crista*, 34—*Gyraulus parvus*, 35—*G. circumstriatus*, 36—*G. deflectus*.

exclusive for some parameters. Thus, with respect to the variables examined, the majority of the species studied could theoretically occur together in the same environment, near the lower end of the concentration scale for inorganic parameters. For example 25 of the species could occur through the entire range of 100–200 mg/liter for total dissolved solids, and an additional eight could occur in portions thereof (Pip, 1986).

Mean niche positions may be regarded as the types of environments for which each species was most characteristic. *Stagnicola reflexa*, *Helisoma corpulentum*, *Bulimnea megasoma*, *Campeloma decisum*, *H. campanulatum*, *Amnicola walkeri*, and *Marstonia decepta* were classified in clusters 1 and 2 in both figures 1 and 2. These species showed low mean values for inorganic concentrations and narrow tolerance ranges; they may be regarded as specialists for environments with low values of these factors. Since the latter environments in the study area are most common on the Precambrian Shield, it is not surprising that these species are also limited to, or most frequent in, Shield waters.

It is interesting that some species showed marked differences in terms of their relative positions in the dendrograms when mean niche positions and niche congruencies were compared. For example *Lymnaea stagnalis*, *Stagnicola palustris*, *Gyraulus deflectus*, and *Helisoma anceps* showed wide niches, but their central tendencies of occurrence were much more moderate. Indeed *G. deflectus* tended to occur most often at the low end of its ecological range, perhaps because it does not compete well with the numerous other species which frequent higher inorganic concentrations.

Species with similar mean niche positions, contained in the same clusters in figure 1, would be expected to compete with each other more frequently than with species in neighboring clusters, because they would be likely to occur in the same water bodies more often. Thus, although each species occupies a unique ecological niche (Hutchinson, 1957), the clusters of adaptively similar species could be viewed as functional groups (*e.g.*, Stanley, 1979) which, on average, respond to certain aspects of the environment in similar ways. However, species within the same clusters in figure 1 often showed differences in niche congruency in figure 2. For example, the species comprising cluster 2 in figure 1 showed similar mean niche positions located at lower inorganic concentrations, but of these species, *Marstonia decepta* was included in cluster 1 in figure 2, *Ferrissia rivularis* and *Cincinnatia cincinnatiensis* in cluster 3, *Helisoma pilsbryi infracarinatum* in cluster 4, and *Gyraulus deflectus* in cluster 5. Such differences in the ecological ranges of species with similar central tendencies of occurrence may have been advantageous in that the reduced overlap alleviated competition (*e.g.*, Hughes, 1980), since the proportion of cases where the two species would not be able to occur together was increased.

The most common species in the study area [*i.e.*, *Physa gyrina* (61.9% of sites sampled), *Lymnaea stagnalis* (60.7%), *Helisoma trivolvis* (45.3%), *Stagnicola palustris* (40.5%), *Gyraulus parvus* (39.5%)] (Pip, 1987) showed broad tolerance ranges for the variables examined, and can occupy a wide variety of habitats. These species would be expected to compete with each other frequently, since large portions of their niches were congruent. However, they occurred most commonly at different mean positions within their niches. Of these five species, which clustered in two adjacent groups in terms of niche congruency (figure 2), only *L. stagnalis* and *H. trivolvis* occurred in the same cluster in terms of mean niche position (figure 1).

Nonetheless, because of the large amount of overlap, species with similar niches and broad ranges still often coexisted in the same water bodies. For example, the five most common species above were significantly associated with each other in the study area (Pip, 1978). Such species with large proportions of niche overlap may minimize competition where they coexist by partitioning the habitat. For example *G. parvus*, a small species, feeds primarily on periphyton, while the larger of the common species also ingest macrophyte tissue, and may favor

separate macrophyte species within the same water body (Pip & Stewart, 1976). Interspecific differences in diet have also been reported by Reavell (1980). Other types of habitat partitioning may occur in certain situations, for example with respect to depth (Lacoursiere *et al.*, 1975), temperature (Boag, 1981), and turbulence (Calow, 1973).

The proportionally greater niche differences between species found at low inorganic concentrations were reflected by the lack of significant association between the species in clusters 1 and 2 in figure 2 at the same sites within the study area [except for *M. decepta* and *H. campanulatum* (Pip, 1978)]. Greater niche differences in unproductive environments may have been associated with more intense competition (Emlen, 1973) than in nutrient-rich situations, where niches among many species were similar, and a number of interspecific associations were observed. Eutrophic waters show greater productivity of algae and macrophytes, which constitute much of the food of freshwater gastropods (Reavell, 1980). Food has been proposed as an important factor regulating gastropod abundance and distribution (*e.g.*, Dillon & Benfield, 1982). Species richness of gastropod communities in the study area is positively correlated with trophic state (Pip, 1987). This correlation derives from the tendencies of many species to occur more often at higher values of phosphorus (Pip, 1978, 1986), despite the observation that most of the species can also tolerate low values of this factor.

Competition has been put forward as an important factor governing gastropod distribution (*e.g.*, Lassen, 1975). Species which are taxonomically and morphologically similar (*i.e.*, "sibling species") (Aho *et al.*, 1981) often were not grouped within the same clusters with respect to niche similarity (*e.g.*, the species of each *Stagnicola, Fossaria, Helisoma*) (figures 2 and 3), indicating intrageneric ecological differentiation, while other congeners (*Gyraulus circumstriatus* and *G. deflectus*) were grouped together. Aho *et al.* (1981) found a similar lack of consistency in the distributions of gastropods in Finnish lakes and suggested that competition is only one of a number of factors that contribute towards distribution.

Conversely, most of the groupings which emerged in figures 2 and 3 contained a wide representation of different taxonomic and morphological entities. Accordingly, while the niches within each group were similar with respect to the parameters examined, species behavior and ecological requirements were likely to be different, decreasing competition. Furthermore, differences with respect to other parameters may also have been important, for example type of water body and bottom substrate (Pip, 1986), type of vegetation (Pip, 1978), or other, unmonitored, chemical and physical variables.

Principal component analysis yielded a representation of the species in a hyperspace, of which the first two dimensions accounted for more than three-quarters of the variance. While the first dimension was clearly related to the types of chemical environments in which the species most often occurred, the groupings in figure

3 also reflected the geographical distributions and types of habitats frequented by the respective species. Species in groups A and B were present largely in Precambrian Shield waters characterized by low total dissolved solids, and were absent or rare west of the Shield boundary. Species in group C frequented ponds and small lakes (Pip, 1986) with intermediate water chemistry values. Group D occurred frequently in lakes. Group E species occurred in a very wide variety of water chemistry types, and differed with respect to preferences for water body type, in some cases lacking discernable preferences entirely. Species in group F occurred in the most extreme ranges of water chemistry, but were found most frequently in ponds (Pip, 1986).

While the niche means and widths utilized here are those observed for the study area as a whole, ecological ranges may vary for a given species in different geographical regions (Pip, 1985), and are likely different for individual populations. The importance of particular parameters may also vary among habitats with different chemical and physical characteristics (Pip, 1987). Thus the exact position of the niche may be a plastic attribute that can vary to some extent with situation as well as time.

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Factors Affecting the Distribution of Sphaeriid Bivalves in Britannia Bay of the Ottawa River

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ABSTRACT

Distribution of Sphaeriidae in Britannia Bay of the Ottawa River was not homogeneous and was primarily affected by sediment particle size and depth. Total sphaeriid diversity is maximal at particle sizes near 0.18 mm. Total sphaeriid density and abundance of the genus *Pisidium* increase with decreasing water depth. Distribution of species within the genera *Pisidium* and *Musculium* is variable. These data indicate that comparisons of pisidiid distribution should consider at least depth, and particle size in the sampling design.

INTRODUCTION

The importance of sphaeriids as part of the aquatic community has lead to a number of studies dealing with the distributional patterns of this group (Healey, 1978; Mackie *et al.*, 1980). Most studies, however, have dealt with distribution patterns among a group of lakes, rivers, or sections of a river. Usually it is assumed that variation among sites is greater than the variation within sites. However, data in Avolizi (1976) and Holopainen (1979) suggest that the abundance of some species can be variable within a single site, but little work has been done to determine the extent of this variation.

Britannia Bay, a section of the Ottawa River just above Ottawa and Hull, Canada, is relatively unpolluted, and is known to contain a diverse sphaeriid fauna (15 species), including members of *Musculium*, *Pisidium*, and *Sphaerium* (Mackie, 1971). The purpose of this study was to determine if the depth distribution of sphaeriids in Britannia Bay is homogeneous, and if distribution is a function of the sediment particle size, organic matter content, algal biomass, and depth.

MATERIALS AND METHODS

During mid-August, 1985, benthos and sediment samples were taken at eight depths (0.25, 0.35, 0.50, 1.0, 2.0, 3.0, 4.0, and 6.0 m) along a transect in Britannia Bay of the Ottawa River (figure 1).

At each depth, five Ekman grab (15 × 15 cm, 0.32 mm mesh screen on top) samples were taken, except at 0.36 m where four samples were taken. A sediment sample was taken at each depth from which three subsamples (approximately 100 ml) were taken. Two for determination of percent organic matter content and one for geometric mean particle size.

From each benthic sample, all sphaeriids and algae (entangled masses of *Lyngbya* sp. and *Vaucheria* sp.) were hand picked. Sphaeriids were counted and identified to species. Algae was dried at 70 °C and weighed to the nearest 1.0 mg. Total sphaeriid diversity (Shannon & Weaver, 1949) and density (N/m^2), and individual species abundances were calculated for each benthic sample.

The organic content of the sediments was estimated by ashing two of the sediment samples from each depth and expressing the result as percent loss on ignition. Geometric mean particle size was determined with the third sediment sample from each depth using the methods outlined by Lotspeitch and Everest (1981).

Stepwise multiple regressions (Ostle & Mansing, 1975) were performed to determine which environmental factors significantly affected total sphaeriid diversity and density, and the abundances of individual genera and species. Only those variables found to be independent by simple correlations (table 1), were used coincidentally in the regression models.

Box plots (McNeil, 1977) determined that all data, except diversity values, were most normally distributed when the depth means were transformed by $\log_{10}$. All simple correlations and stepwise multiple regressions were calculated using the normalized data.

RESULTS

Depth means of algal biomass, and % organic matter content are presented in figures 2 and 3. Both parameters increased with increasing water depth. Trends in sediment particle size are given in figure 4. Compared to other depths, sediments were coarser at the 1.0, 2.0, and 6.0 m depths.

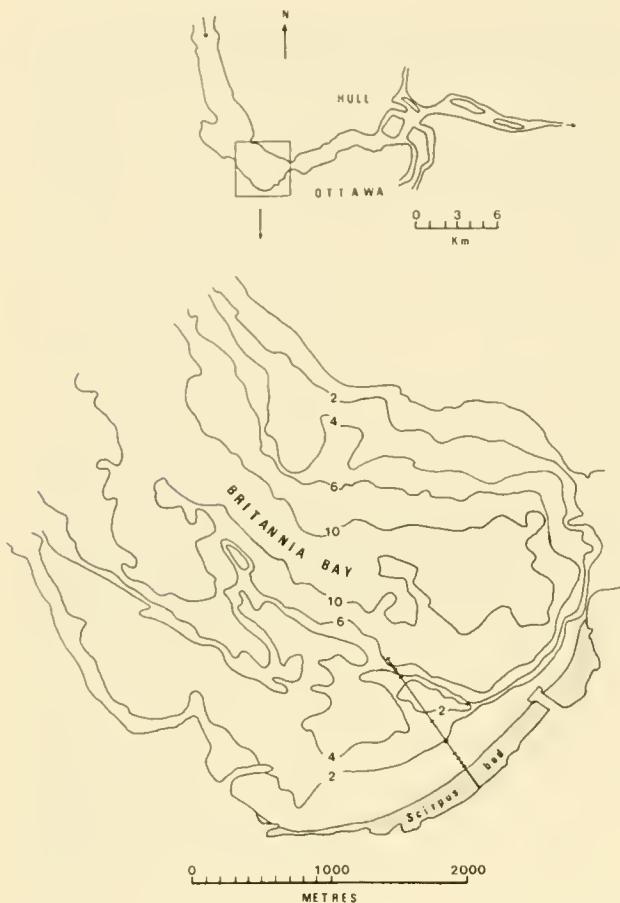Twelve sphaeriid species were found in Britannia Bay

Figure 1. Map of the Ottawa River, and an enlarged map of Britannia Bay above Ottawa indicating location of the transect. Depth contours on enlarged map are in metres.

with *P. casertanum* the most abundant species. Mean abundances at each depth for each species are presented in table 2.

Diversity values were highest at the shallow depths (0.25–0.50 m) and at 3.0 and 4.0 m (figure 5). Stepwise multiple regression indicated that diversity increased with decreasing particle size (table 3). Figure 6 indicates a unimodal distribution of diversity in relation to geometric mean particle size. Maximum diversity occurred near a particle size of 0.18 mm.

Regression analysis indicated that total sphaeriid density significantly increased with decreasing water depth

Table 1. Correlations between some environmental variables. Significant correlations ($P < 0.05$) are indicated by asterisks (*).

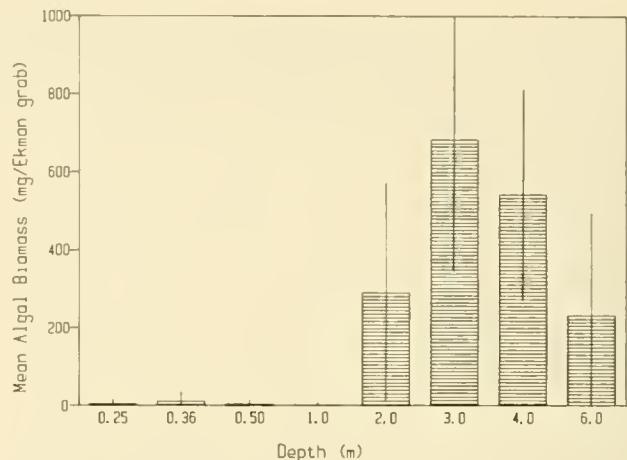|	Algal biomass	Organic matter	Depth
Organic matter	0.787*		
Depth	0.839*	0.863*	
Particle size	0.152	−0.043	0.322

Figure 2. Mean algal biomass at each depth along the transect with 95% confidence limits indicated by vertical lines.

(table 3). Density at 0.25 m was less than that at 0.36 and 0.5 m (figure 7).

Abundance of the genus *Pisidium* significantly increased with decreasing water depth (table 3). A similar relationship was found for *P. variabile*. Abundance of *P. casertanum* significantly increased with finer sediments and lower organic matter content. None of the other seven *Pisidium* species were correlated with the environmental variables.

Abundance of the genus *Musculium* did not correlate with any of the variables tested. Abundance of *M. transversum* increased significantly with decreasing water depth (table 3). Abundance of *M. securis* correlated positively with algal biomass.

No relationship was found for the genus *Sphaerium* which was represented by only one species, *S. striatinum*.
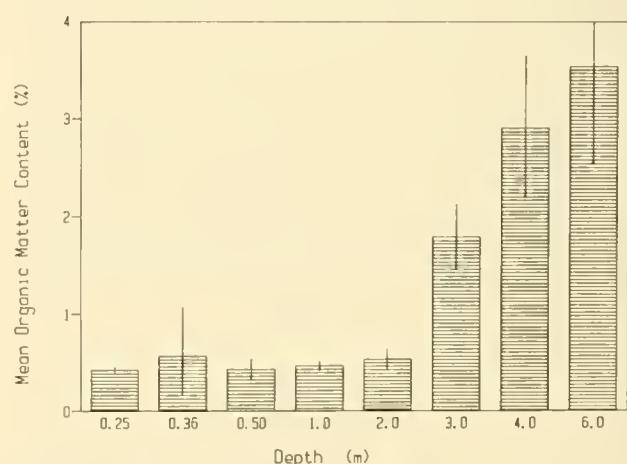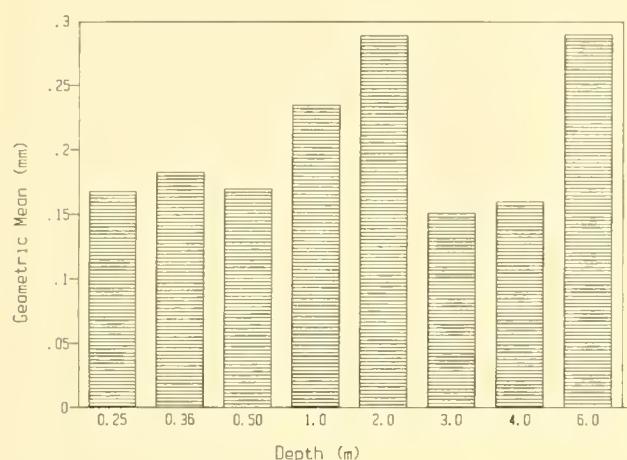

Figure 3. Mean organic matter content of the sediments at each depth along the transect with 95% confidence limits indicated by vertical lines.
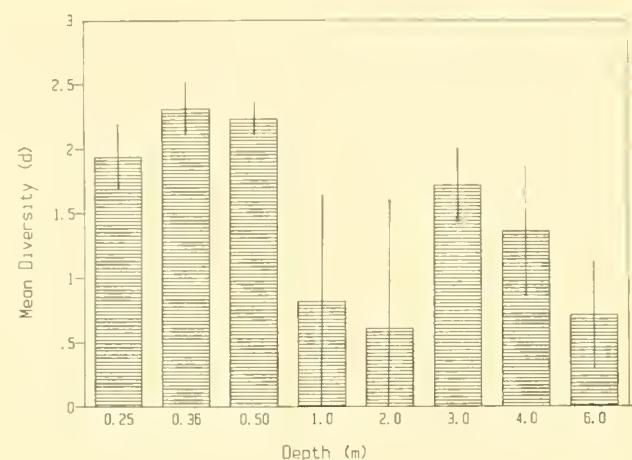
Figure 4. Geometric mean particle size at each depth along the transect.

Figure 5. Mean diversity values at each depth along the transect with 95% confidence limits indicated by vertical lines.

DISCUSSION

In Britannia Bay, total sphaeriid diversity significantly increases with finer sediments. The finer sediments at 3.0 and 4.0 m, which correspond with high diversity values, contradict the positive correlation which exists between particle size and depth in rivers (Hamill, 1975). The sand bar between the 3.0 and 4.0 m sites (figure 1) may have affected the distribution of sediments in the same manner that Folke and Ward (1957) describe for a sand bar in the Brazos River.

The unimodal distribution of diversity in relation to particle size (figure 6) indicates that diversity is maximal at a particle size near 0.18 mm, and decreases with finer or coarser material. Finer substrates enhance burrowing

(Rogers, 1976), production (Hamill, 1975), growth and reproduction (Mackie & Qadri, 1978), and may improve survival in young clams (Gale, 1976). Fine substrates, however, may reduce oxygen availability (Meier-Brook, 1969; Hartnoll, 1983). The particle size at which diversity is maximized may represent the optimal grain size for efficient burrowing and/or oxygen, nutrient availability.

Total sphaeriid density increases in shallow water in Britannia Bay. From the literature, it appears that resource availability and utilization may be affected by depth. Bacteria and phytoplankton (especially diatoms), which are food resources for sphaeriids (Holopainen, 1985), are generally more abundant in shallow water (0–2.0 m) than in deep water (> 5.0 m) (Hargrave, 1970).

The drop in total sphaeriid density at 0.25 m which

Table 2. Mean abundance (No./m²) of individual species at each depth along the transect.

Species	Depth (m)								Total no. sampled
	0.25	0.36	0.5	1.0	2.0	3.0	4.0	6.0	
Musculium									
M. securis (Prime, 1852)	17.8	0	8.9	0	88.9	80.0	115.5	35.6	39
M. transversum (Say, 1829)	444.4	266.6	26.6	8.9	17.8	0	0	0	80
Pisidium									
P. casertanum (Poli, 1795)	942.1	1,833.2	1,173.2	35.6	17.8	142.2	106.7	0	437
P. dubium (Say, 1816)	17.8	11.1	26.7	0	8.9	0	8.9	0	8
P. ferrugineum (Prime, 1852)	0	22.2	44.4	0	0	8.9	0	0	8
P. henslowanum (Sheppard, 1823)	0	188.9	168.9	0	0	0	8.9	0	37
P. lilljeborgi (Esmark and Hoyer, 1886)	124.4	600.0	1,262.1	8.9	8.9	35.6	88.9	35.6	230
P. nitidum (Jenyns, 1832)	231.1	944.4	1,528.7	0	0	17.8	26.7	26.7	291
P. punctatum (Sterki, 1895)	133.3	422.2	160.0	0	0	8.9	17.8	8.9	75
P. variabile (Prime, 1852)	106.7	100.0	195.5	8.9	0	0	0	0	44
P. walkeri (Sterki, 1895)	0	11.1	0	0	0	0	0	0	1
Sphaerium									
S. striatinum (Lamarck, 1818)	0	0	195.5	26.7	35.6	231.1	62.2	17.8	64
Total no. sampled	227	396	539	10	20	59	49	14	1,314
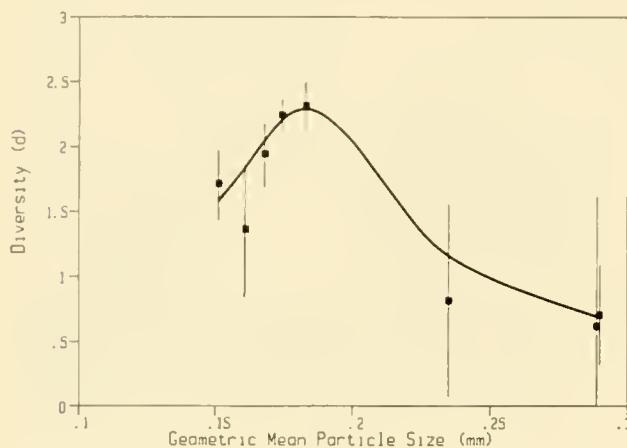
Figure 6. Relationship between mean diversity and geometric mean particle size with 95% confidence limits indicated by vertical lines.

Figure 7. Mean density at each depth along the transect with 95% confidence limits indicated by vertical lines.
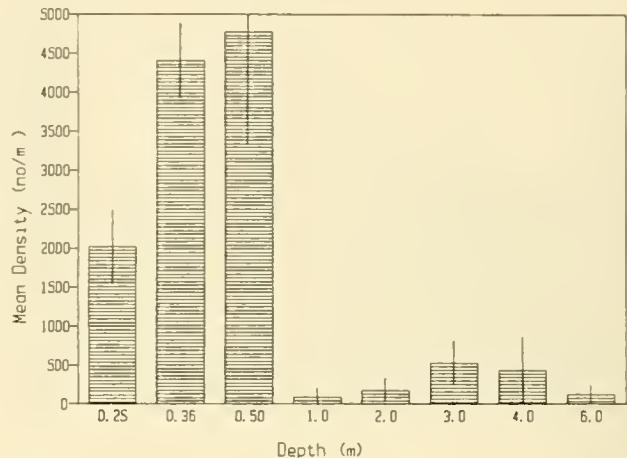
is inconsistent with the regression model, may result from wave action and/or summer lethal temperatures, which can significantly reduce the numbers of sphaeriids in the shallower areas in Britannia Bay (Mackie, 1971; Mackie & Qadri, 1978).

Regression analysis suggests that the genus *Pisidium* prefers shallower water in Britannia Bay. The relationship between *P. variabile* and depth is consistent with the distribution of the genus. In contrast, *P. casertanum* prefers finer substrates with lower organic matter content. The distribution of *P. casertanum* suggests that there can be variability in the distributional patterns of species within a genus.

That the distribution of the genus *Musculium* is not related to any of the variables tested may be due to variation in the distribution patterns of the two species of *Musculium*. Competition between *M. securis* and *M. transversum* in Britannia Bay, as described by Mackie *et al.* (1978), may also be responsible for these results. It is likely that two species are not sufficient to determine a general distribution pattern of a genus.

Table 3. Significant relations between the dependent variables (D) and the independent variables (I), where, R = correlation coefficient between D and I, a = algal biomass, b = depth, c = geometric mean particle size, and d = % organic matter content of the sediments.

D	I	R (D, I)	Significance level
Total sphaeriid diversity	c	−0.791	$P < 0.020$
Total sphaeriid density	b	−0.720	$P < 0.050$
Musculium securis	a	0.819	$P < 0.025$
Musculium transversum	b	−0.940	$P < 0.010$
Pisidium	b	−0.733	$P < 0.030$
Pisidium casertanum	c	−0.711	
	d	−0.614	
	total R^2 =	0.883	$P < 0.010$
Pisidium variabile	b	−0.939	$P < 0.010$

The positive relationship between abundance of *M. securis* and algal biomass has also been described by Mackie and Qadri (1978) who suggested that *M. securis* utilizes the algae *Lyngbya* and *Vaucheria* as food resources in Britannia Bay. The variability in the distribution of the two species of *Musculium* may also be related to the food forms with which the clams are associated.

That the abundance of the genus *Sphaerium* and most *Pisidium* species do not correlate with the environmental variables may be a result of modal relationships with these variables, or relationships with variables that were not tested. The relationships found centre on the importance of particle size and depth, which have been shown by Green (1971) to be important factors affecting distribution of sphaeriids among lakes. It is suggested that in studies dealing with the distribution of sphaeriids, particle size and depth are important factors to be considered in the sampling design.

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Hypselostoma holimanae New Species, a Pupillid Land Snail from Thailand

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ABSTRACT

Hypselostoma holimanae new species (Gastropoda, Pulmonata, Pupillacea, Vertiginidae) is described from a limestone range near Kanchanaburi, Thailand. Its morphological characteristics are distinct to the extent that no close relationship between this form and other members of the genus is apparent. *Hypselostoma tubiferum* (Benson, 1856) from Burma is it closest phylogenetic and geographic congener. The two species are alike in details of sculpture and umbilical width, but differ widely in shell shape and aperture barriers. Similarities of reduced apertural dentition among other species of *Hypselostoma* are considered to be due to convergence.

INTRODUCTION

The land snail fauna of Thailand is very poorly known. The genus *Hypselostoma* is widely distributed from Burma through Cambodia, Vietnam, Malaya, the Loo Choo Islands and the Philippine Archipelago. Yet not a single species has hitherto been recorded from Thailand. The species described in this paper was collected by Stephen C. Holiman while serving as a Peace Corps volunteer in Thailand. During his few opportunities of leisure, Mr. Holiman collected mollusk specimens for his mother, Mrs. Stanley (Bonnie) Holiman of Jacksonville, Florida, who has assembled a private collection of fair importance because of the data that accompanies the specimens. The mollusks from Thailand were submitted to us by Mrs. Holiman for identification. The new species of *Hypselostoma* described in this paper shows strong similarity to the generic type species from Burma, and differs conspicuously from other known species. We are honored to name this snail after Mrs. Holiman in recognition of her bringing this species to our attention.

Hypselostoma holimanae new species
(figures 1–6)

Description: Shell small, about 2.6–2.9 mm wide and 2.3–2.6 mm high; about 0.85–0.95 times as high as wide. Shell turban-shaped with a moderately long conical spire (figures 1–3, holotype). Last whorl conspicuously enlarged, and with a distinct peripheral angle and a basal angle. Last whorl flat below peripheral angle, and strongly shouldered above. Occasional specimens may be weakly furrowed below periphery. Last whorl ascending at about 10° to longitudinal axis of spire (figures 2, 4). Neck of last whorl becoming narrowed behind aperture, and extending forward for about $\frac{1}{5}$ of minor diameter of last whorl (figure 3); indented externally over junction of angulo-parietal lamella and slightly so over columellar lamella. Base of shell broadly umbilicate due to lateral expansion of last whorl. Umbilicus about 0.40–0.53 times minor diameter of last whorl as measured across the basal angle. Whorls 4.6–4.9. Protoconch consisting of about 1.5 whorls that appear smooth under light microscopy; at higher magnifications the whorls are sculptured with a dense mesh of fine reticulating threads that have an underlying spiral arrangement (figure 5). Whorls of teleoconch sculptured with raised spiral threads that are nearly uniformly distributed over the surface of the shell (figure 4). Threads weak but distinct on spire; most conspicuously developed on last whorl (figure 6). Spiral threads interrupted at irregular intervals by incremental growth striations, which in some specimens may cause the spiral sculpture to appear cancellate or beaded on the spire. Color dark brown with a light brown aperture and white lamellae within the aperture. Face of aperture translucent with fine radiating brown lines due to raised spiral threads on opposite surface Peristome broadly expanded and nearly uniformly wide around aperture. Aperture barrier with four teeth located on inner rim of the aperture just behind expanding peristome and arranged opposite each other in a cross-configuration. Angulo-parietal lamella rectilinear, forming a single short undulating blade; bifid as is typical for genus, with angular segment smaller and separated from parietal portion by a weak notch. Palatal and basal plicae short and laterally flattened; confined to inner rim of peristome. Columellar lamella tubercular and located on a slight callus.
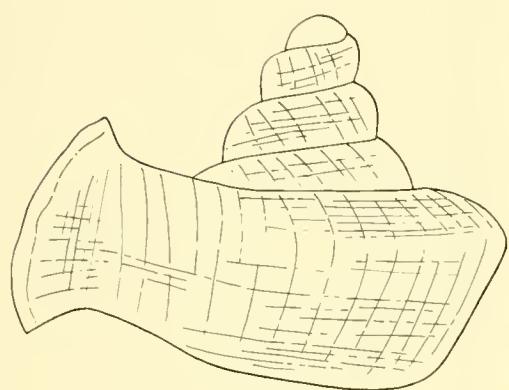
Measurements in mm for the holotype and three paratypes (UF 113428) selected to show variation follow. The minor diameter is the transverse width of the body whorl posterior to the neck of the aperture. Other measurements were made of standard parameters.
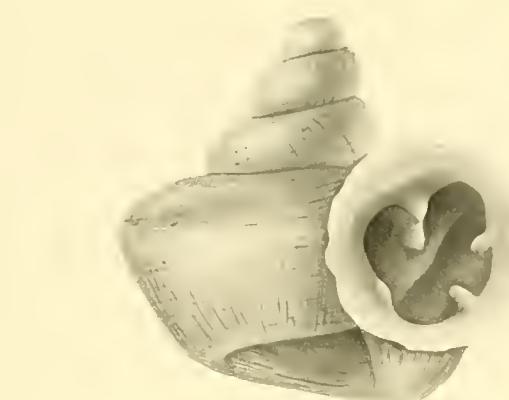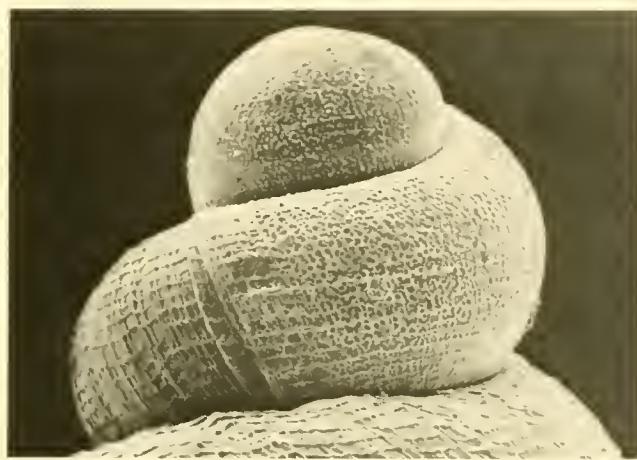
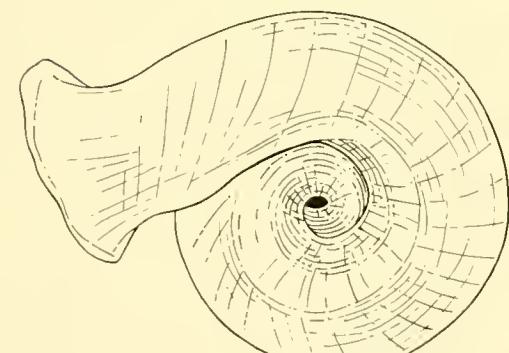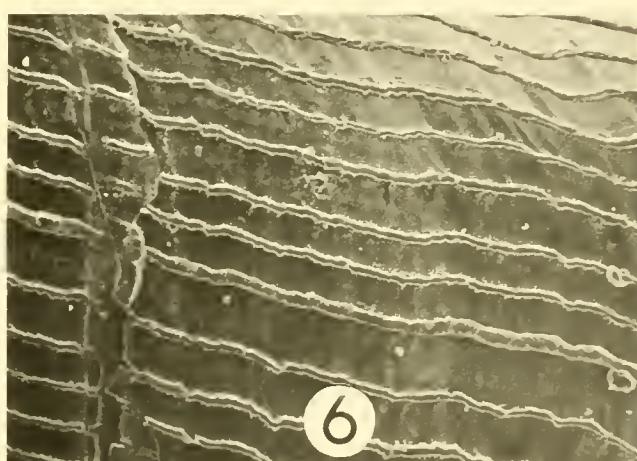**Figures 1–6.** *Hypselostoma holimanae* new species. **1–3.** Holotype (UF 113427). × 26. **4–6.** Paratype (UF 113483). **4.** × 40. **5.** × 120. **6.** × 160.

Specimen	Height	Maj. w	Min w	Aper w	Umbil	Whorls
Holotype	2.4	2.6	2.4	1.4	1.2	4.7
Paratype	2.3	2.7	2.3	1.4	0.9	4.8
Paratype	2.3	2.6	2.3	1.2	1.0	4.6
Paratype	2.6	2.9	2.5	1.6	1.0	4.9

Type locality: Thailand, Kanchanaburi Province, small limestone range on the west border of the Kanchanaburi Agricultural College, about 15 km west of Kanchanaburi. Holotype: UF 113427; collected March 15, 1987 by Stephen Holiman. Paratypes: UF 113428 (12), UF 113483, Mahidol University Malacology Collection, Bangkok (12), and the private collections of Harry G. Lee (12) and Bonnie Holiman (12).

The specimens constituting the type series are recently dead shells. They were collected at the height of the dry season from leaf-litter in a forested knoll at the top of the limestone range.

COMPARISONS

Hypselostoma Benson, 1856 belongs to a group of genera that also includes *Boysidia* Anvey, 1881, *Paraboysidia* Pilsbry, 1917, *Gyliotrachela* Tomlin, 1930, *Aulacospira* Moellendorff, 1890, *Anauchen* Pilsbry, 1917, and *Systenostoma* Bavay and Dautzenberg, 1909. These genera were monographed by Pilsbry (1917). More recently, Jutting (1950) reviewed the known species of the first four genera. Members of this group have protoconch sculpture similar to that described above for *H. holimanae*. The variation of this sculpture within the group and its phylogenetic significance will be discussed elsewhere (Thompson, in preparation). The classification of species within these genera is sometimes problematic, and no one who has worked with the group seems to have been comfortable with the systematic arrangements of previous authors (Pilsbry, 1917; Jutting, 1950, 1961; Solem, 1981; Thompson & Dance, 1983). Much of the problem centers on the emphasis that is placed on the development of the parietal and angular lamella, the reduction of the aperture barrier, the sculpture on the teleoconch and the degree to which the aperture is attached to or free of the previous whorl. *Hypselostoma holimanae* is placed within *Hypselostoma* because of the fused angulo-parietal lamella, the free aperture and the spiral sculpture of the teleoconch. The angulo-parietal lamella is weaker than in most other species of the genus, and the aperture barrier in general approaches the condition that characterizes *Anauchen*. However, all of the species of *Anauchen* lack any indication of an angular lamella and none have raised spiral sculpture on the teleoconch.

Few species of *Hypselostoma* have thus far been described from the mainland on southeast Asia. Pilsbry (1917) discussed the species known at that time. More recently, Jutting (1950) briefly reviewed the genus and described several additional species (1950, 1961, 1962). *Hypselostoma*, as used by both Pilsbry and Jutting, is a polyphyletic assemblage that contains species belonging to at least three genera. Four species (*H. terae* Tomlin,

1939, *H. megaphona* Jutting, 1949, *H. elaphis* Jutting, 1949, *H. perigyra* Jutting, 1949) were transferred to *Boysidia* (*Dasypupa*) by Thompson and Dance (1983:109). Three others related to *H. dayanum* Stoliczka, 1871 belong in another genus (Thompson, in preparation).

The remaining species placed in *Hypselostoma* differ strikingly from *H. holimanae*, although *H. tubiferum* (Benson, 1856) from Burma appears to be the most closely related congener. It has a similarly broad umbilicus and similar spiral sculpture on the teleoconch, though not as strong. Because of these similarities the two species are considered to be more closely related than either is to other known species within the genus. The two differ in several conspicuous features. *Hypselostoma tubiferum* is much more depressed, the aperture is turned upward above the apex of the spire and the aperture barrier consists of 6–7 lamellar teeth (see Pilsbry, 1917 for a description and illustrations). *Hypselostoma holimanae* differs from all other mainland species by its strong spiral sculpture, its reduced aperture barrier with tubercular columella lamella, its strong circumumbilical basal keel, and its broad umbilicus. Some Philippine species (*H. sibuyanicum* Moellendorff, 1896, *H. quadrasi* Moellendorff, 1896, *H. roebeleni* Moellendorff, 1894, and *H. latispira* Thompson and Auffenberg, 1984) are similar to *H. holimanae* in that the aperture barriers have been reduced to denticles, although they are not as weak as in *H. holimanae*. None has sculpture as strongly developed as *H. holimanae*, none has a basal keel circumscribing the umbilicus, nor are any as widely umbilicate. Other differences that separate *H. holimanae* from these Philippine species are the shape of the shell and the contour of the whorls. *Hypselostoma roebeleni* and *H. latispira* are very depressed species in which the upturned aperture reaches almost to the level of the apex of the spire. *Hypselostoma sibuyanicum* and *H. quadrasi* have more slender shells with regularly increasing whorls, and both are narrowly rimate. The combination of all of these morphological differences indicate that the similar aperture barriers of the Philippine species and *H. holimanae* have evolved independently through tooth reduction from more complex ancestral conditions, and that no close relationship can be inferred on the basis of these barriers.

ACKNOWLEDGEMENTS

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Eledone gaucha, a New Species of Eledonid Octopod (Cephalopoda: Octopodidae) from Southern Brazil

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ABSTRACT

A new species of *Eledone* is described from the southwestern Atlantic at depths of 60 to 160 m, off Rio Grande do Sul, Brazil. The characters that distinguish this species from the other species of the genus are presented, as well as a morphometric comparison with the sympatric *Eledone massyae* Voss, 1964.

INTRODUCTION

Several cephalopods were collected during a survey of the demersal resources of the inner shelf of Rio Grande do Sul between Solidão (30°40'S) and Chui (34°20'S) at depths to 100 m (figure 1) by the R/V "Atlântico Sul" of Fundação Universidade de Rio Grande (FURG). Haimovici and Andriguetto (1986) stated that two species of the octopod genus *Eledone* were found. One of them, *E. massyae*, was described by Voss (1964) and the second was a new species. Both sympatric species possess the generic character of papillae at the tips of the non-hectocotylized arms of the males. Morphological analysis presented here as well as biochemical differences found by Levi *et al.* (1985) separate these two similar species.

MATERIALS AND METHODS

All specimens studied were killed with fresh water, fixed in 10% formalin for 24 hr and preserved in 70% ethanol. Measurements were taken in millimeters, and all measurements and indices used are among those described by Roper and Voss (1983). The drawings of *E. gaucha* are by Jose Angel Alvarez Perez. The types are deposited in the Museu Oceanografico de Rio Grande (MORG), Museu Nacional de Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museo Nacional de Historia Natural, Uruguay (MNHN), Museo de Ciencias Naturales de La Plata, Argentina (MCNLP), University of Miami Mollusks Laboratory (UMML) and National Museum of Natural History, Smithsonian Institution (USNM).

Eledone gaucha new species
(figures 2–14, table 1)

Material examined: Holotype: ♂ 32.5 mm ML, R/V Atlântico Sul, cruise 13/83, Sta. 37, 32°58'S, 51°19'W, 56 m, trawl, 17 Nov. 1983, MORG 23544. Paratypes: 7 ♂ 27–41 mm ML and 5 ♀ 32–34 mm ML, R/V Atlântico Sul, cruise 13/83, Sta. 37, 32°58'S, 51°19'W, 56 m, trawl, MORG 23544; 2 ♂ 32–34 mm ML, R/V Atlântico Sul, cruise 13/83, Sta. 39, 32°50'S, 50°45'W, 87 m, trawl, 18 Nov. 1983, MORG 23545; 1 ♂ 21 mm ML, R/V Atlântico Sul, cruise 13/83, Sta. 2, 31°46'W, 100 m, 9 Nov. 1983, MORG 23846; 1 ♀ 33 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 51, 33°43'S, 52°13'W, 60 m, trawl, 29 Aug. 1983, MORG 23547; 4 ♀ 28–33 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 57, 33°13'S, 51°25'W, trawl, 60 m, 30 Aug. 1983, MORG 23548; 1 ♂ 33 mm ML and 1 ♀ 44 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 53, 33°52'S, 51°55'W, 52 m, trawl, 29 Aug. 1983, UMML 32.2066; 1 ♂ 34 mm ML and 1 ♀ 42 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 53, 33°52'S, 51°55'W, 52 m, trawl, 29 Aug. 1983, USNM 816613; 1 ♂ 26 mm ML and 1 ♀ 29.5 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 51, 33°43'S, 52°13'W, 74 m, trawl, 29 Aug. 1983, MZUSP 25242; 1 ♂ 32 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 55, 32°52'S, 51°43'W, 140 m, trawl, 30 Aug. 1983, MCNLP 4681; 1 ♀ 29.5 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 57, 33°13'S, 51°25'W, 60 m, trawl, 30 Aug. 1983, MCNLP 4682; 1 ♂ 30 mm ML and 1 ♀ 38 mm ML, R/V Atlântico Sul, cruise 10/83, Sta. 53, 32°52'S, 51°55'W, 52 m, trawl, 29 Aug. 1983, MNHN 14762, MNHN 14763; 1 ♂ 35 mm ML and 1 ♀ 42 mm ML, R/V Atlântico Sul, cruise 3/83, Sta. 42, 33°02'S, 51°30'W, 130 m, trawl, 17 June 1980, MNRJ 5626, MNRJ 5627.

DESCRIPTION

Animal small, maximum observed mantle length 65 mm (figures 2, 3). Mantle firm, not very thick, ovoid and elongated (MWI ♂: 61.0; ♀: 59.2) separated from head by small constriction. Body surface smooth with some papillae on the dorsal mantle and head. Head narrower than mantle (HWI ♂: 36.2; ♀: 37.3); eyes slightly protuberant. One supraocular cirrus. Funnel long (FLI ♂: 44.6; ♀: 45.4) with anterior half free (FFuLI ♂: 21.6; ♀: 21.1); funnel organ (figure 4) W shaped.

Arms long and rather slim. Arms length order 1>2>3>4 in most specimens with dorsal arms markedly longer than others. All arms longer in males (except hectocotylized arm) than in females (ALI I to IV ♂: 273.2–239.8–134.9–208.1; ♀: 250.0–213.8–200.6–191.0).

Suckers small, uniserial, well separated and deeply set into arms. Suckers somewhat crowded near tips of the arms on females. Two rows of minute fleshy papillae on all non-hectocotylized arms of males (figure 10). Number of suckers on basal half of the first right arms varies from 17 to 23 (ASC ♂: 20.1; ♀: 19.4), suckers slightly larger on all arms of males (IASI ♂: 7.7; ♀: 6.5).

Web extends over half the length of arms and decreases from dorsal to ventral surface; web formula most frequently A:B:C:D:E. Web indices similar in both sexes; 24.4–24.1–21.6–18.6–15.6 for males and 24.4–23.9–21.1–18.3–14.9 for females.

Third right arm in males hectocotylized (figure 9) (HcAI: 58.9). Ligula small (LLI: 8.8), without differentiated calimus (figure 9); spermatophore grove deep.

Gill count in external hemibranch from 7 to 10, most frequently 8 in males and 9 in females (Gilc ♂: 8.2; ♀: 8.9).

Males reproductive system with no special figures (figure 11). Penis long and tubular (PLI: 23.4) with a rather short diverticulum (PdLI: 7.8). Spermatophores undifferentiated (figure 13) from 12 to 20 mm (SpLI: 45; SpLWI: 1.56). Number of spermatophores in a sample of 40 mature males from 7 to 92 (mean 32.1).

The proximal oviduct long, the oviductal glands small, the distal oviducts shorter and somewhat stouter (figure 12). Intraovaric eggs oval (figure 14); maximum lengths of apparently mature eggs approximately 8 mm. Number of developing eggs in a sample of 42 maturing females ranged 10–55 (mean 30.2).

Buccal mass well developed, with small anterior salivary glands and larger posterior salivary glands. Esophagus connects to developed crop leading to muscular stomach and smaller spiral caecum united by two ducts to the large digestive gland. Intestine thin and leads to the anus adjacent to ink sac opening. Ink sac superficially embedded in the digestive gland (figure 7). Radula with a tricuspid rachidean tooth, three lateral teeth and a marginal plate (figure 8).

Color of living animals changed from brown to almost white dorsally always remaining clear ventrally. Color of specimens preserved in alcohol purplish gray dorsally and pale yellow ventrally. Inner surface of the arms, mouth, and ventral mantle with few chromatophores.
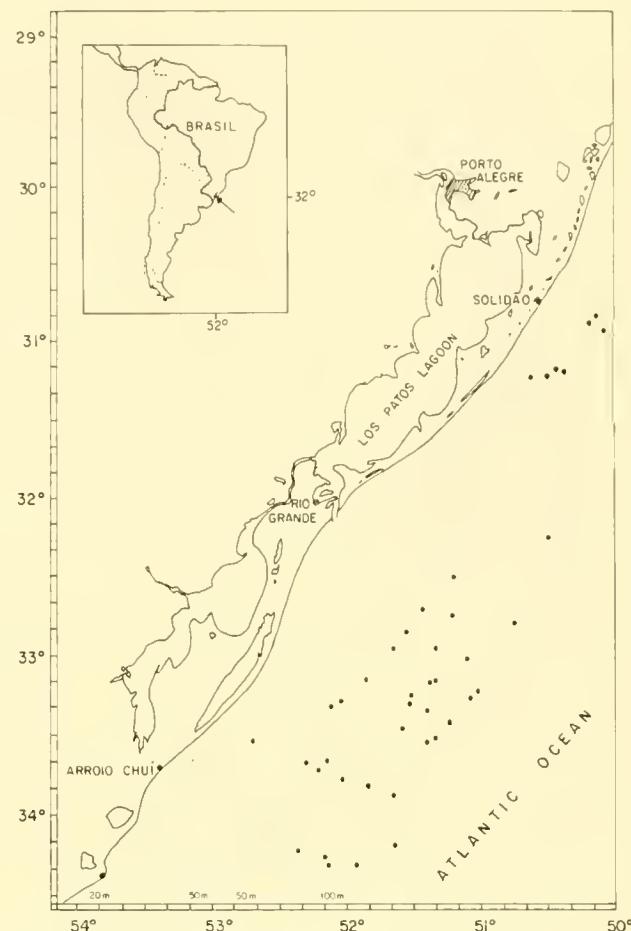

Figure 1. Sample localities of *Eledone gaucha* new species.

Type locality: 32°58′S, 51°19′W, south Rio Grande, Brazil in 56 m.

Etymology: The name *gaucha* refers to the coastal planes of Argentina, Uruguay, and southern Brazil and its people.

Distribution: *Eledone gaucha* is known only from off Rio Grande do Sul between Solidao (30°40′S) and Chui (34°20′S) (figure 1).

DISCUSSION

The new species belongs in the genus *Eledone* because of a single row of suckers, the heteromorphic arms in the males, with the non-hectocotylized arms having the suckers at their tips modified into fleshy papillae or laminae, and the hectocotylus without a differentiated calimus. These characters distinguish *Eledone* from related genera *Pareledone*, *Vosseledone*, *Graneledone* and others (Palacio, 1978).

The genus *Eledone* occurs on the Atlantic continental shelves of South America, Africa, and Europe and in the Mediterranean Sea. It includes six described species: *E. moschata* (Lamarck, 1798) and *E. cirrhosa* (Lamarck,
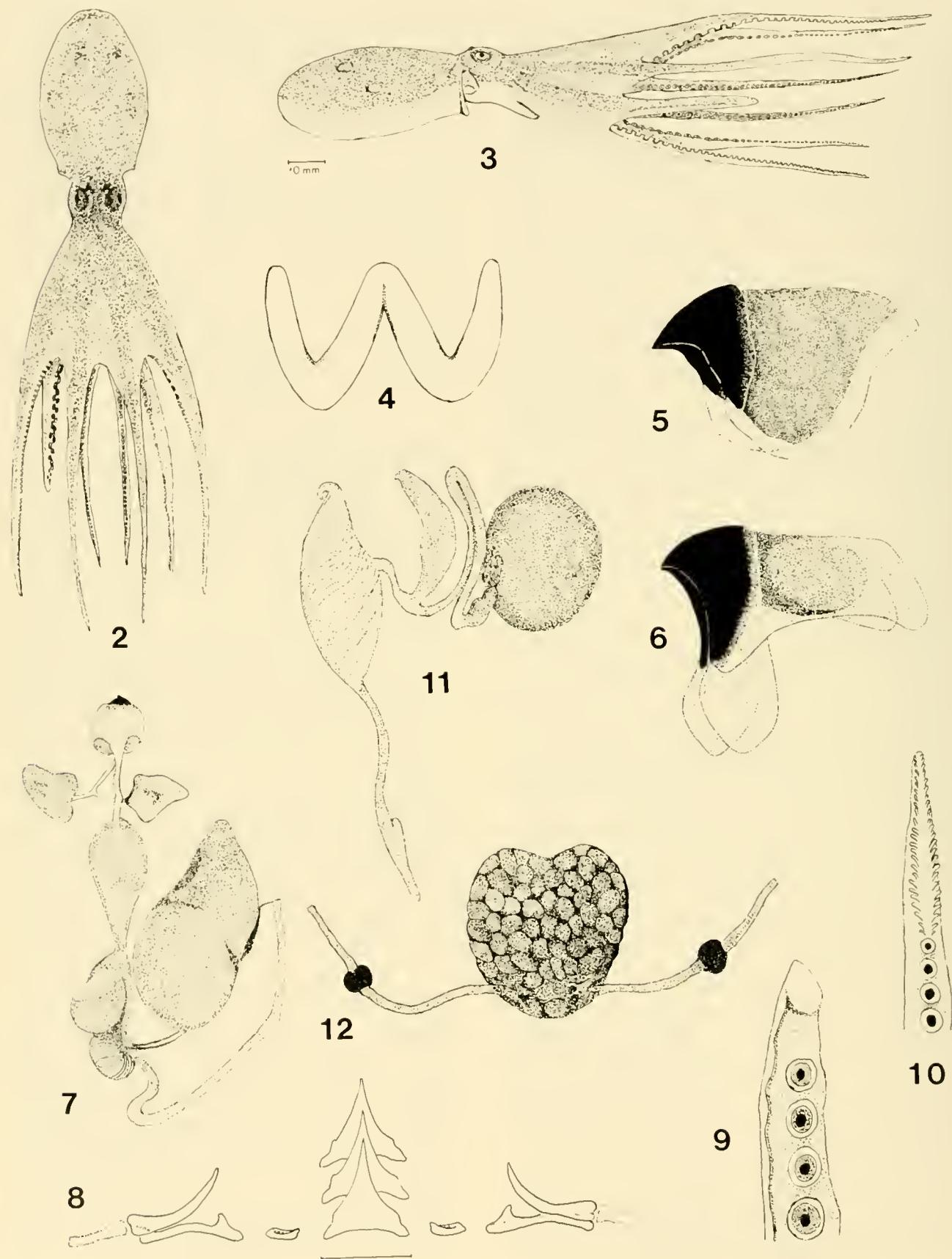
Table 1. Ranges and means of measurements and indices of 10 males and 10 females each of *Eledone massyae* Voss, 1964 and *Eledone gaucha* new species, from southern Brazil.

| Index | *Eledone massyae* Voss, 1964 | | | | | | *Eledone gaucha* new species | | | | | |
| | Males | | | Females | | | Males | | | Females | | |
	Lower limit	Mean	Upper limit	Lower limit	Mean	Upper limit	Lower limit	Mean	Upper limit	Lower limit	Mean	Upper limit
Total length (TL)	148.0	176.4	207.0	195.0	218.2	236.0	81.0	123.2	137.0	100.0	131.9	178.0
Mantle length (ML)	45.0	54.0	63.0	60.0	65.3	71.0	21.0	31.6	41.0	28.0	35.5	50.0
Mantle width index (MWI)	65.1	76.2	88.2	75.8	79.3	88.9	47.6	61.0	71.9	40.0	59.2	70.0
Head width index (HWI)	40.4	47.4	56.5	38.2	41.9	45.0	34.2	37.5	40.0	28.0	36.2	43.6
1° right arm length index (I ALI)	184.0	201.4	216.0	185.0	209.9	247.0	244.0	275.2	322.0	227.0	250.0	284.0
2° right arm length index (II ALI)	195.0	203.3	235.0	190.0	217.3	248.0	193.0	239.8	281.0	162.0	213.8	242.0
3° right arm length index (III ALI)	155.0	199.1	225.0	185.0	214.1	252.0	85.0	134.9	159.0	155.0	200.6	236.0
4° right arm length index (IV ALI)	191.0	204.0	224.0	186.0	215.5	243.0	134.0	208.1	256.0	162.0	191.0	213.0
Arm formula (AF)		4:2:1:3			2:4:3:1			1:2:3:4			1:2:3:4	
A web depth index (A WDI)	19.1	24.3	28.5	19.8	22.5	27.4	16.8	24.2	30.9	18.9	24.4	28.6
B web depth index (B WDI)	18.2	24.5	27.5	21.0	23.8	29.6	19.0	24.1	30.1	18.9	23.9	25.8
C web depth index (C WDI)	22.9	25.9	28.3	21.2	24.1	28.9	18.8	21.6	28.9	17.6	21.1	23.7
D web depth index (D WDI)	22.7	24.8	28.6	20.9	24.3	27.6	14.6	18.6	23.0	15.8	18.3	20.5
E web depth index (E WDI)	13.4	20.6	25.3	18.6	20.8	22.9	11.5	15.6	21.6	12.3	14.9	17.4
Web formula (WF)		C:D:B:A:E			D:C:B:A:E			A:B:C:D:E			A:B:C:D:E	
Gill lamellae count (GiLC)	8/10	9.4/9.2	11/7	9/10	9.7/9.6	8/10	7/9	8.2/8.5	9/9	8/8	8.9/8.5	10/10
Funnel length index (FLI)	37.8	41.9	45.9	40.8	44.2	48.2	36.6	44.6	51.9	32.5	45.4	51.7
Free funnel length index (FFuLI)	17.5	23.2	29.5	20.9	23.8	27.9	14.6	21.6	31.0	10.0	21.1	30.3
Arm sucker count (ASC)	16	18.1	20	16	17.8	20	17	19.4	22	18	20.1	23
Arm sucker index I (I ASI)	6.3	7.7	9.1	7.0	7.9	8.7	4.7	7.7	9.3	6.0	6.5	8.0
Arm sucker index II (II ASI)	6.3	8.0	9.1	7.0	8.2	9.6	4.7	7.3	9.3	5.0	6.4	8.0
Arm sucker index III (III ASI)	5.5	7.4	8.9	7.0	7.9	8.5	4.7	7.6	9.6	5.0	6.0	7.5
Arm sucker index IV (IV ASI)	5.5	7.2	8.9	6.7	7.7	8.4	4.7	6.7	7.8	3.0	5.1	6.7
Penis length index (PLI)	19.3	28.1	39.3				19.5	23.4	28.1			
Penis diverticulum length index (PdLI)	6.6	15.0	22.2				4.9	7.8	10.5			
Spermatophore length index (SpLI)	20.9	31.6	37.7				38.3	45.0	50.0			
Spermatophore width index (SpWI)	1.8	2.5	3.1				1.2	1.6	2.1			
Hectocotylized arm index (HcAI)	59.0	69.2	81.4				41.7	58.9	67.4			
Ligula length index (LLI)	5.3	8.0	9.7				4.9	8.8	12.5			

179S) both from the NE Atlantic and Mediterranean, *E. thysanophora* Voss, 1962 and *E. caparti* Adam, 1950 from the SE Atlantic, and *E. massyae* Voss, 1964 and *E. gaucha* from the SW Atlantic.

Eledone gaucha seems to be a relatively abundant species off Rio Grande do Sul. The possible reasons why it has not been recognized to date are its small size, its similarity to *E. massyae*, and the scarcity of scientific cephalopod collections by research vessels in this area. Due to its small size it is not retained in the cod ends of commercial trawlers and even in the R/V Atlântico Sul surveys it most often was found entangled in the wings of the net. Palacio (1977) reviewed several museum collections of Argentina, Uruguay, and Brazil and found

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Figures 2–12. Anatomical features of *Eledone gaucha* new species. **2, 3.** Dorsal (2) and lateral (3) views of holotype (MORG 23544, 32 mm ML). **4.** Funnel organ. **5.** Upper mandible. **6.** Lower mandible. **7.** Digestive tract. **8.** Radula. **9.** Hectocotylized arm tip. **10.** Non-hectocotylized arm tip of male. **11.** Male reproductive organs. **12.** Female reproductive organs.
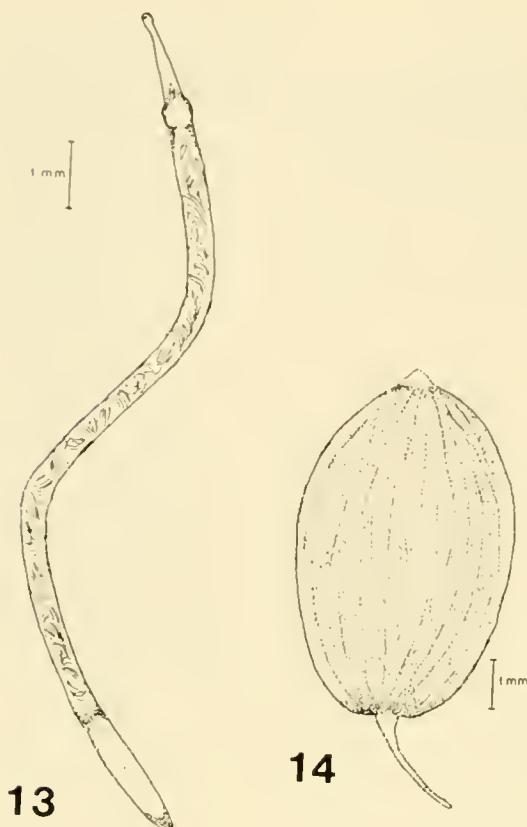
Figures 13, 14. Reproductive products of *Eledone gaucha* new species. 13. Spermatophore. 14. Egg.

only one eledonid, *E. massyae*. A survey of the MORG collection by the author showed one specimen of *E. gaucha* (MORG 15341) formerly classified as *E. massyae*. It is expected that reviews in other collections will expand the range of *E. gaucha*.

The sympatric species *E. massyae* and *E. gaucha* initially look similar but many differences may be seen in a more detailed study. In order to compare both species morphologically, the same indices were calculated for 10 males and 10 females of *E. massyae* (collected in the same survey) which were fixed, preserved, and measured in the same way as the new species (table 1). *Eledone gaucha* is smaller and has a narrower mantle and head. The arms are thinner, longer, and decrease in size while in *E. massyae* all arms are approximately the same length. The hectocotylized arm is shorter and the web depth decreases from the dorsal to the ventral surface in *E. gaucha*, while in *E. massyae* the web is shorter only between the ventral arms. The funnel organ is W shaped in *E. gaucha*, vv shaped in *E. massyae*. The number of inner and outer gill lamellae is one unit lower and the arms sucker count two units higher in *E. gaucha*. Arm sucker indices are similar in males of both species, but in females they are smaller in *E. gaucha*. Perhaps the best single diagnostic character to distinguish mature males of both species is the spermatophore, which is

shorter and much thinner in *E. gaucha*. Externally, the best distinctive character is the arm length pattern.

Eledone caparti was described by Adam (1950) based on five specimens, two males and three females colle~ted in the equatorial west Africa at depth ranging from 60 to 170 m. No figures or tables were included in the original description. The decreasing arm length and web depth of *E. caparti* are similar to those of the new species. However, *E. caparti* does not have a supraocular cirrus, has enlarged suckers at the base of the lateral arms of the males, and the number of suckers on the dorsal arms is almost double that in *E. gaucha*. The radula of *E. caparti* has an A2 seriation and the spermatophore is insufficiently described for comparisons.

Eledone thysanophora was described by Voss (1962) based on a single male specimen collected in a tide pool in western South Africa. The morphometric description is short, but the number of papillae on the tips of the non-hectocotylized arms and the structure of the spermatophore, with the inner wall of the horn portion lined with teeth, differentiate *E. thysanophora* from the new species.

Summary descriptions of *E. cirrhosa* (Lamarck, 1798) and *E. moschata* (Lamarck, 1798) are presented in Roper *et al.* (1984), and the species are compared by Rees (1956). Both species can be distinguished from *E. gaucha* by several characters. *Eledone cirrhosa* has moderately short arms, a ridge along the mantle, non-hectocotylized arms of males with a single row of compressed sucker-like cirri, and spermatophores with spines. *Eledone moschata* has subequal arms, 11 to 12 filaments on the outer hemibranch of the gills, big, sausage-shaped eggs 15 mm long, and a characteristic musk odor.

ACKNOWLEDGEMENTS

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News and Notices

54TH ANNUAL MEETING OF THE AMERICAN
MALACOLOGICAL UNION
CHARLESTON, SOUTH CAROLINA
RADISSON FRANCIS MARION HOTEL
June 19–24, 1988

The 54th annual meeting of the American Malacological Union will be held June 19–24, 1988 in Charleston, South Carolina. Charleston is a historical city, many parts of which have been beautifully restored, as has the Radisson Francis Marion Hotel, which is located downtown, within walking distance of many restaurants, shops and other attractions. Charleston is easily accessible both by air and by interstate highway.

Three symposia are planned: Applications of Nucleic Acid Techniques to the Study of Molluscan Evolution, convened by Dr. M.G. Harasewych, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution; Systematics and Evolution of Non-marine Mollusks, convened by Dr. Robert Hershler, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution; and History of Malacology, convened by Dr. W. Backhuys, E.J. Brill, Inc. Leyden, The Netherlands.

In addition to these symposia, contributed papers and poster presentation, scheduled events will include a tour of historic Charleston, guided field trips to terrestrial and marine molluscan communities, an auction to benefit the symposium fund, and a banquet.

For further information, please contact:

Richard E. Petit
President, AMU
P.O. Box 30
North Myrtle Beach, SC 29582 USA
Telephone (803) 249-1454

16TH CONCHOLOGISTS OF AMERICA
CONVENTION
FORT MYERS, FLORIDA
SHERATON HARBOR HOUSE HOTEL
July 11–15, 1988

The 16th convention of the Conchologists of America is scheduled for July 11–15, 1988. This convention will be headquartered in the Sheraton Harbor House Hotel in Fort Myers, Florida, and hosted by the Southwest Florida Conchologist Society. Convention activities are centered around informative, shell-related programs, fascinating field trips and interesting tours. A fund-raising auction, dealer's bourse, and banquet are all planned. A field trip to the Sarasota Fossil Pits is scheduled for Saturday, July 16, 1988.

Pre-registration forms and packets for the Convention, Hotel and Field Trip reservations are available from:

Gene Herbert
19168 Meadow Brook Court N.W.
North Fort Myers, FL 33903 USA
Telephone (813) 731-2405

or

Al Bridello
2265 West Gulf Drive # 240E
Sanibel, FL 33957
Telephone (813) 472-1637

INSTRUCTIONS TO AUTHORS

THE NAUTILUS publishes papers on all aspects of the biology and systematics of mollusks. Manuscripts describing original, unpublished research as well as review articles will be considered. Brief articles, not exceeding 1000 words, will be published as notes and do not require an abstract. Notices of meetings and other items of interest to malacologists will appear in a news and notices section.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted in triplicate. Text must be typed on one side of 8½ × 11 inch white paper, double spaced throughout (including literature cited, tables and figure captions), with at least 1 inch of margin on all sides. All pages must be numbered consecutively. If printed on a word processor, the right margin should be ragged rather than justified. Authors should follow the recommendations of the *Council of Biology Editors Style Manual*, which is available from the Council of Biology Editors, Inc., 9650 Rockville Pike, Bethesda. MD 20814, U.S.A. The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Latin names and words to be printed in italics must be underlined; leave other indications to the editor. Metric and Celsius units are to be used.

The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgements, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

All line drawings must be in black, high quality ink, clearly detailed and completely labeled. Photographs must be on glossy, high contrast paper. All figures are to be consecutively numbered (figs. 1, 2, 3, . . . , NOT figs. 1a. 1b, 1c, . . . NOR plate 1, fig. 1 . . .). Illustrations must be arranged in proportions that will conform with the width of a page (6¾ inches or 171 mm) or a column (3¼ inches or 82 mm). The maximum size of a printed figure is 6¾ by 9 inches or 171 by 228 mm. All illustrations must be fully cropped, mounted on a firm, white backing, numbered, labeled and camera ready. The author's name, paper title and figure number(s) should appear on the back. Original illustrations must be between one and two times the desired final size. It is the author's responsibility that the line weight and lettering are appropriate for the desired reduction. Original illustrations will be returned to the author if requested. Color illustrations can be included at extra cost to the author.

Voucher Material: Deposition of type material in a recognized public museum is a requirement for publication of papers in which new species are described. Deposition of representative voucher specimens in such institutions is strongly encouraged for all other types of research papers.

Processing of Manuscripts: Upon receipt, every manuscript is acknowledged and sent for critical review by at least two referees. These reviews serve as the basis for acceptance or rejection. Accepted manuscripts are returned to the author for consideration of the reviewers' comments. A finalized version of the manuscript is returned to the editor and sent to press. Two sets of proofs are sent to the author for correction. Changes other than typesetting errors will be charged to the author at cost. One set of corrected proofs should be sent to the editor as soon as possible. Authors with institutional, grant or other research support will be billed for page charges at the rate of $55.00 per printed page.

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Manuscripts, corrected proofs and correspondence regarding editorial matters should be sent to: Dr. M.G. Harasewych, Editor, Division of Mollusks, NHB stop 118, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA.

THE NAUTILUS

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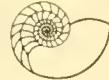NAUTILUS, P.O. Box 3430, Silver
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CONTENTS

A New Species of Pleurotomariid Gastropod from the Western Atlantic

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ABSTRACT

Perotrochus charlestonensis, a new species of pleurotomariid, is described from off the coast of South Carolina. This is the 12th Recent pleurotomariid taxon to be described from the western Atlantic. Its habitat is described, environmental data are provided, and comparisons made with closely related congeners.

Key words: Gastropoda; pleurotomariid; *Perotrochus*; slit shells; western Atlantic; JOHNSON-SEA-LINK.

INTRODUCTION

Since the discovery of the first living species of the predominantly Mesozoic and Paleozoic family Pleurotomariidae in the western Atlantic over a century ago (Fischer & Bernardi, 1856), 24 Recent species and subspecies have been described, usually on the basis of one or a very few specimens. The habitat of these animals, generally steep-walled, hard substrates at depths in excess of 100 meters, accounts for their infrequent collection by such methods as trawling, dredging, and grab sampling, and, therefore, for the paucity of data on the biology and distribution of most species. Since the publication of a review of the Recent pleurotomariids that included six species from the West Indies (Bayer, 1966), three species (Bayer, 1967; Rios & Mathews, 1968; Leme & Penna, 1969) and two subspecies (Okutani & Goto, 1983, 1985) have been described from the western Atlantic.

Another new species of pleurotomariid, described herein, was collected while conducting fish population studies approximately 90 nautical miles east of Charleston, South Carolina, utilizing the submersible JOHNSON-SEA-LINK I (Harbor Branch Oceanographic Institution, Inc., Fort Pierce, Florida). Bottom topography at the study area was extremely rugged, making sampling by any other means difficult.

SYSTEMATICS

Family **Pleurotomariidae** Swainson, 1840
Genus *Perotrochus* P. Fischer, 1885

Perotrochus charlestonensis new species
(figure 1)

Description: Shell (figure 1) moderately large (maximum diameter 87.4 mm, minimum diameter 80.1 mm, height 73.0 mm), broadly turbiniform, very thin, fragile; spire angle 89°, spire slightly convex in profile; protoconch of 1.0 whorls, translucent, glassy; transition to teleoconch marked by axial costae, with selenizone apparent by second postnuclear whorl; teleoconch of 8⅓ whorls; early whorls nearly flat-sided, becoming progressively more inflated; selenizone near suture in early whorls, shifting to slightly below mid-whorl by fifth postnuclear whorl; anal slit depth at upper margin 89°, at lower margin 57°; anal slit width 4 mm; suture adpressed; periphery rounded; base inflated, convex, non-umbilicate; nacreous umbilical callus extending ⅕ the distance from axis to periphery; spiral sculpture of 21 uniformly sized spiral cords between suture and anal slit, 20 cords of variable thickness between anal slit and periphery, 40 cords along base; selenizone with 0–5 broad cords, number increasing with shell size; axial sculpture of weak nodes on early whorls (88 on fourth postnuclear whorl), forming cancellate sculpture; axial sculpture decreasing, sculpture limited to spiral cords by sixth postnuclear whorl above selenizone, and seventh postnuclear whorl below selenizone; aperture broadly ovate; columellar lip slightly thickened, weakly recurved; color creamy white with diffuse brownish orange axial streaks and blotches; nacreous layer visible through porcellaneous layer, creating iridescent hue; color lighter on base than on dorsal surface; selenizone margins with cream colored lines most evident on penultimate and body whorls; aperture nacreous, iridescent; operculum multispiral (7 whorls), horny, brownish-yellow, translucent; soft parts unknown.

Type locality: 90 nautical miles east of Charleston, South Carolina (32°43'80"N, 78°05'60"W), in 213 m, R/S JOHNSON-SEA-LINK I, dive 1250, August 6, 1982.

Holotype: USNM 859961, maximum diameter 87.4 mm.

Etymology: Named after the type locality, commonly referred to as the Charleston Lumps.

Figure 1. *Perotrochus charlestonensis* new species. Apertural, right lateral, apical, and basal views of the holotype (USNM 859961), off Charleston, South Carolina (32°43′80″N, 78°05′60″W), in 213 m, maximum shell diameter 87.4 mm.

Ecology: This species is known only from the type lo-cality, an area of extremely rugged terrain where the bottom topography consists of steep, large hills and val-leys. Topographical features (figure 2) consist of a pave-ment of relithified phosphorite and fibrous concretionary apatite composed of calcium phosphate and other min-erals (Manheim *et al.*, 1980). This pavement, which ranges in thickness from 10 cm to almost a meter, has been undermined in some areas, causing large pieces to break off and fall down-slope forming rubble and boulder zones. Hills range in height from several meters to about 30 meters. Valleys contain sand composed primarily of brown

to black phosphorite. This area was formed during the middle Tertiary and has remained stable since the Mio-cene (Baturin, 1982).

Marine life in the vicinity indicates an area of high productivity resulting from warmer Gulf Stream waters. Large snowy grouper [*Epinephelus niveatus* (Valen-ciennes, 1828)] and blue-lined tile fish [*Caulolatilus mi-crops* (Goode & Bean, 1878)] are abundant in the area together with many species of small, deep-reef fish, which generally inhabit rocky terrain. Common invertebrates include basket and brittle stars, sea urchins, solitary and colonial anemones, solitary corals, arrow, spider, and gal-
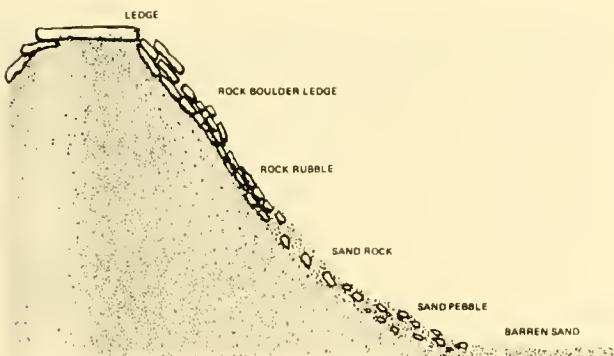
Figure 2. Cross-section of bottom topography at collection site. Hills range in height from 3 to 30 m.

atheid crabs, barrel and encrusting sponges, and hydroids. A pink featherlike hydroid covers many of the broken boulders along the ridge tops. Prevalent gastropods include *Perotrochus amabilis* (Bayer, 1963), *Calliostoma sayana* (Dall, 1889), *Stenorhytis pernobilis* (Fischer & Bernardi, 1857), *Aurinia gouldiana* (Dall, 1887), and *Pterynotus phaneus* (Dall, 1889).

Remarks: *Perotrochus charlestonensis* is a member of the species complex consisting of *P. midas* Bayer, 1966, *P. pyramus* Bayer, 1967, *P. africanus* (Tomlin, 1948), *P. teremachii* (Kuroda, 1955), *P. tangaroana* Bouchet & Metivier, 1982, and an undescribed species from off northwestern Australia (Group B, Bayer, 1966:745). All are characterized by having large, thin shells with inflated whorls and proportionally large, broadly ovate apertures. This new species most closely resembles *P. africana* and *Perotrochus* sp. (Bayer, 1966: fig. 29) from Japan, but differs from these taxa in having a thinner shell with more inflated whorls, and a more convex profile of the spire. *Perotrochus africanus* has a more stepped spire, a more strongly recurved and thicker columella, and a broader umbilical callus (¼ distance from axis to periphery). Of the western Atlantic species, *P. charlestonensis* is most similar to *P. pyramus*, but is more than twice the size, and is much higher-spired. *Perotrochus charlestonensis* also somewhat resembles *Perotrochus midas*, but lacks its characteristic flat, blunt spire and angular periphery. *Perotrochus charlestonensis* occurs in shallower water (213 m) than either *P. pyramus* (420–648 m) or *P. midas* (600–770 m).

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Spongivory in Pleurotomariid Gastropods

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ABSTRACT

Direct *in situ* observations of feeding together with analyses of the gut contents of *Perotrochus midas* and *P. amabilis* indicate that these species feed predominantly and selectively on sponge tissue. Foraminiferal and diatom tests previously reported in the gut contents of pleurotomariids are derived from planktonic sediment coating the surfaces of sponges and do not significantly contribute to the nutrition of these gastropods. The family Pleurotomariidae represents an adaptive radiation to spongivory that most likely occurred after the divergence of the herbivorous Scissurellidae and Haliotidae from the pleurotomariid progenitor in the late Paleozoic, but prior to the appearance of umbilicate pleurotomariids with deep anal canals in the Upper Jurassic.

Key words: Pleurotomariidae; diet; sponges; spongivory; *Perotrochus*; *Mikadotrochus*; *Entemnotrochus*.

INTRODUCTION

Since the discovery of the first living species of the family Pleurotomariidae in the mid-nineteenth century, numerous papers have been published on various aspects of the biology and anatomy of these, the most primitive living gastropods (*e.g.*, Bouvier & Fischer, 1899, 1902; Woodward, 1901; Fretter, 1964, 1966; Yonge, 1973; Hickman, 1984a,b). As pleurotomariids are predominantly restricted to hard substrates and bathyal depths in the Recent fauna, sampling has proved difficult and most published observations are based on limited material, often poorly preserved.

The common occurrence of sponge spicules, foraminiferal tests, and diatoms in the alimentary systems and fecal pellets of pleurotomariids has been variously interpreted as being indicative of a spongivorous diet consisting of a single species of sponge (Woodward, 1901: 252); a diet consisting principally of sponges (Thiele,

1935:1129; Hyman, 1967:360; Yonge & Thompson, 1976: 52); a diet of encrusting invertebrates, predominantly sponges (Hickman, 1984a:29); or detrital feeding and vegetarian diet (Fretter & Graham, 1976:1). The presence of sponge spicules in the gut contents, however, is not necessarily evidence of spongivory. Although members of the pleurotomariacean family Haliotidae are known herbivores (Leighton, 1961; Leighton & Boolootian, 1963; Shepherd, 1973; Fretter & Graham, 1976: 6), Leighton and Boolootian (1963:229) reported sponge spicules, comprising 1–2% of the gut content volume, in 25–50% of the specimens of *Haliotis cracherodii* they examined. Similarly, Herbert (1987:289) identified sponge spicules, foraminiferans, annelid setae, and crustacean remains in the alimentary systems of members of the Solariellinae (Trochidae), a group adapted to feeding on superficial and interstitial detritus. Three species of pleurotomariids maintained in aquaria have been reported to feed on a wide variety of foods, including starfish, bivalve meat (Arakawa *et al.*, 1978) and sliced, raw fish (Matsumoto *et al.*, 1972; Sekido *et al.*, 1976).

The increasing use of research submersibles in deep sea investigations has made possible *in situ* observations on the feeding of two species of pleurotomariids. These observations, supported by gut content analyses of collected voucher material, form the basis of this report.

MATERIALS AND METHODS

During the course of numerous dives aboard the research submersible JOHNSON-SEA-LINK-II throughout the northern and central Bahamas, living *Perotrochus midas* Bayer, 1966, were observed on 16 occasions at depths ranging 670 to 853 meters. Observations were noted and specimens photographed when practical, using a BEN-THOS 35 mm camera, with 85 mm lens. Two of the

Figures 1, 2. *Perotrochus midas* Bayer, 1966, and *Strongylophora hartmani* Van Soest, 1981, *in situ*. 1. *Perotrochus midas* feeding on *Strongylophora hartmani*, JSL-II dive 1501, #2, west end of Island at Gouldings Cay, New Providence Island, Bahamas, 25°00′00″N, 77°34′06″W, in 766 m. October 20, 1987. Specimen not collected. Note area of sponge consumed by snail. 2. *Perotrochus midas* and *Strongylophora hartmani* along steep wall, JSL-II dive 1505, Chub Cay, Berry Islands, Bahamas, 25°22′22″N, 77°50′25″W, in 777 m. October 23, 1987. Specimen not collected. Note layer of planktonic sediment.

specimens were collected, one together with its prey, using the hydraulic arm and clamshell scoop. These specimens were fixed in formalin and preserved in 70% ethanol.

Fifty-six specimens of *Perotrochus amabilis* (Bayer, 1963) were observed and collected during four dives aboard the research submersible Nekton Delta on the "Charleston Lumps", an area of rough bottom topography approximately 90 miles east of Charleston, South Carolina (32°43'78"–32°44'90"N, 78°05'68"–78°06'00"W) (Askew, 1988:91), at depths ranging from 200 to 230 m. Samples were collected by suction through a 2 inch (51 mm) diameter hose. Specimens were frozen on dry ice and maintained at −80°C.

After identification of the intact sponge on which a specimen of *P. midas* was feeding, a spicule sample for SEM examination was prepared by digesting a portion of the sponge in 70% nitric acid (HNO₃) until only siliceous material remained. Two specimens of *P. midas* and three specimens of *P. amabilis* were dissected, and sections of the esophagus between the esophageal valve, situated behind the buccal mass (Fretter, 1964:181, fig. 5, ov; 1966:609, fig. 2, v), and the long sphincter at the opening of the stomach (Fretter, 1966:609) were excised. Also removed were portions of the rectum (Fretter, 1966: fig. 1, r; 1964: fig. 2, r). These sections were teased apart and examined under a dissecting microscope, then treated with warm diluted bleach (1–2% sodium hypochlorite, NaOCl) to dissolve organic material while leaving the siliceous and calcified remains. The preparations were rinsed in distilled water, filtered through 0.4 μm Nuclepore membrane filters, and the filters mounted directly onto SEM stubs. Samples were coated with carbon and gold, and photographed using a Hitachi S-570 scanning electron microscope. A transverse section of the intact sponge was critical point dried prior to SEM examination.

The following voucher material is deposited at the National Museum of Natural History:

Perotrochus midas: Specimen 2. USNM 857097, JSL-II dive 1501, #2, West end of Island at Gouldings Cay, New Providence Island, Bahamas, 25°00'00"N, 77°34'06"W, in 766 m. October 20, 1987.

Perotrochus amabilis: Specimens 1, 2, and 3. USNM 846900, DELTA Dive 560, 129 km due east of Charleston, South Carolina, USA, 32°43'95"N, 78°05'72"W, in 198–210 m. May 3, 1987.

RESULTS

Of the 16 sightings of *Perotrochus midas*, this species was observed in close proximity to, or actively feeding

upon, the sponge *Strongylophora hartmani* Van Soest, 1980 (class Demospongiae, order Haplosclerida) on six occasions (figures 1, 2). Two specimens of *P. midas* were collected, one (specimen 1) together with the sponge on which it was feeding. The esophagus of both snails was distended and full of sponge tissue. Comparisons of spicules taken from the esophagus of both specimens of *Perotrochus midas* (specimen 1, figure 5) with those of *Strongylophora hartmani* (figures 3, 4) confirmed the identity of the prey species. The rectum of specimen 1 contained spicules of *S. hartmani* (figures 6, 7) as well as spicules tentatively attributed to a species of *Pachastrella* (figure 7). The rectal contents of specimen 2 included spicules of *S. hartmani*, but spicules of an unidentified sponge belonging to the order Hadromerida (figure 8) comprised an estimated 80% of the volume. The contents of the esophagus and rectum from both specimens of *P. midas* consisted almost entirely (estimated >95% by volume) of sponge spicules, with foraminiferal and ostracode tests accounting for most of the other identifiable remains.

Of the 53 specimens of *Perotrochus amabilis* observed and collected, the majority were on phosphorite blocks ranging in size from several centimeters to over a meter in length. Only three specimens were on or near a sponge. In all three instances, the sponge, which was small and roughly spherical (<6 cm diameter), could not be collected. Examination of the contents of the esophagus and rectum of these three specimens revealed a more heterogeneous assemblage of sponge spicules (about 80%), diatoms, and foraminiferal tests (about 20%) (figures 9, 10). In no instance could more than an estimated 50% of the contents of either the esophagus or the rectum be attributed to a single species of sponge.

DISCUSSION

Direct feeding observations as well as gut content analyses indicate that *Perotrochus midas* feeds on the sponge *Strongylophora hartmani* by rasping large, deep depressions (>2 cm diameter, >1 cm depth) in its surface (figure 1). In each of the two specimens dissected, the voluminous esophagus was distended, and contained a corresponding volume (2–3 cm³) of sponge tissue. Rectal contents also consisted almost exclusively of sponge spicules, though from species belonging to the orders Choristida and Hadromerida. The most abundant groups of deep water sponges (in terms of biomass) in the tropical western Atlantic and Caribbean are the orders Haplosclerida and Choristida, with the most common species often being highly silicified (Pomponi, unpublished observations). Although six of the 16 sightings of *P. midas* were on or near a haplosclerid sponge, it is unclear

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Figures 3, 4. *Strongylophora hartmani* Van Soest, 1981. **3.** Transverse section, outer surface at top (SEM), scale bar = 300 μm. **4.** Nitric acid spicule preparation (SEM), scale bar = 200 μm. **Figure 5.** *Perotrochus midas*, contents of mid-esophagus of specimen 1, showing high concentration of *Strongylophora hartmani* spicules (SEM), scale bar = 200 μm. **Figures 6, 7.** *Perotrochus midas*, rectal contents of specimen 1. **6.** *Strongylophora hartmani* spicules (SEM), scale bar = 200 μm. **7.** Spicules of *S. hartmani* as well as of ?*Pachastrella* sp. (arrows) (SEM), scale bar = 200 μm. **Figure 8.** *Perotrochus midas*, rectal contents of specimen 2, with spicules of unidentified sponge, order Hadromerida (arrows) (SEM), scale bar = 200 μm.
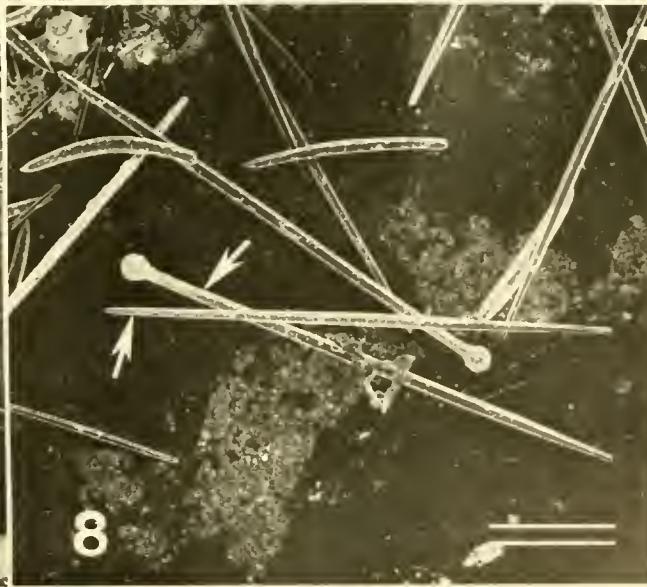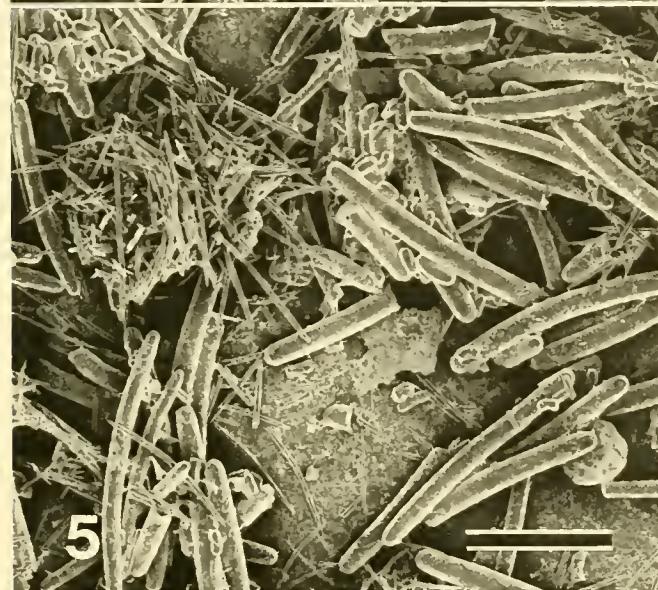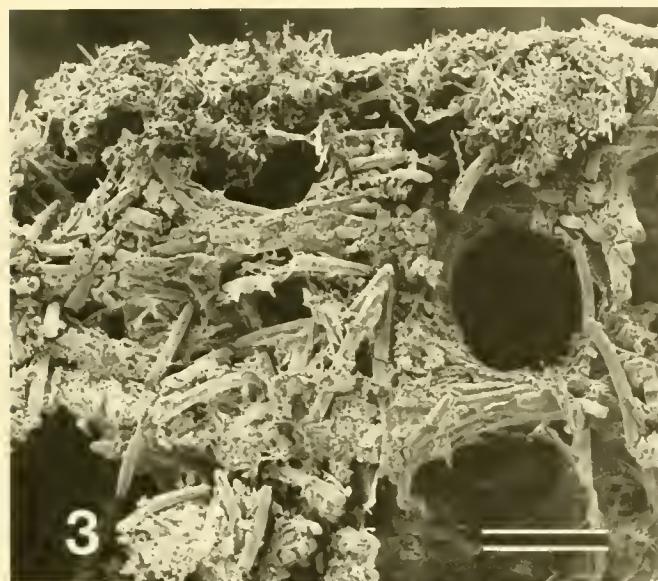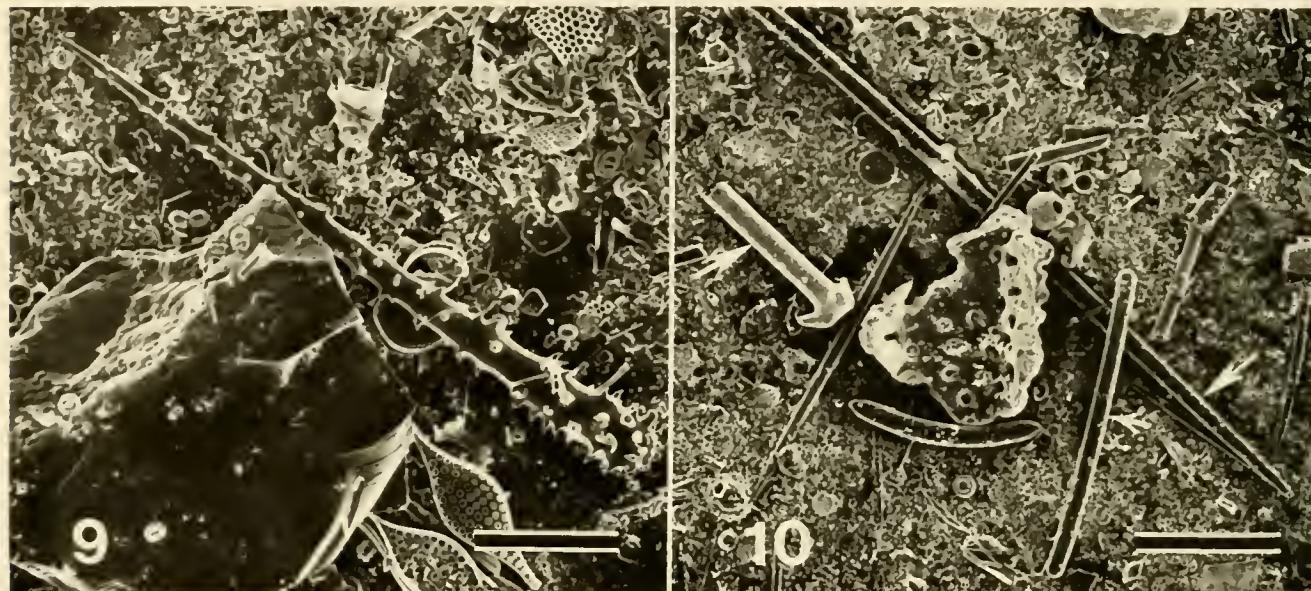
Figures 9, 10. *Perotrochus amabilis* (Bayer, 1963), contents of mid-esophagus of specimen collected 90 miles due east of Charleston, SC, in 210 m. **9.** Spicule of an unidentified species, order Poecilosclerida (SEM), scale bar = 20 μm. **10.** Spicules of *Strongylophora* sp. (small arrow) and an unidentified species, order Choristida or Spirophorida (large arrows) (SEM), scale bar = 100 μm.

whether prey species are selected, or merely reflect the relative abundance of sponges in a nutrient-poor environment. In either case, available evidence indicates that sponges comprise the major component of the diet of *P. midas*, and that the small amounts (<5%) of foraminiferal and ostracode tests as well as other planktonic sediment found in the esophagus and rectum of this species were present on the surface of sponges (figures 1, 2), and probably do not contribute significantly to its nutrition.

Although far more specimens of *Perotrochus amabilis* were observed and collected, fewer were in the proximity of a sponge. Due to the smaller size of this species and the inability to collect the sponges, no direct observations of feeding can be documented. Examination of the contents of the esophagus and rectum of three specimens indicate that sponge spicules comprise approximately 80% of the bleach insoluble mass, the remaining fraction consisting mostly of foraminiferal tests and diatom frustules. Fretter (1964:182) reported similar contents in the stomach of this species and concluded that the animal was a microphagous scavenger. We suggest that *P. amabilis*, like *P. midas*, feed exclusively on sponges, but, due to their smaller size and correspondingly shorter snout, these animals are not able to penetrate as deeply into the tissues of the sponge, and feed on surface tissues covered with deposits of planktonic sediment, thus accounting for the higher proportion of diatoms and foraminifera in the gut.

With a single exception (Barnard, 1963), all published reports on the gut contents of pleurotomariids (table 1) list sponge spicules as a major component. Woodward (1901:252) was the first to speculate that the distinctive radula, shared by all pleurotomariids, was adapted for spongivory, with the hooked teeth "tearing away great pieces of the sponge", and the brush teeth used to "rasp away some of the flesh from the spicules". The occurrence of brush or filament-tipped teeth, long considered unique to Pleurotomariidae, in unrelated, sponge-feeding mesogastropods of the genus *Seila*, has led Hickman (1984a:35) to conclude that this tooth morphology is a functional adaptation to sponge predation and not a phylogenetically constrained, conservative, morphological feature.

Although exceptions have been documented (*e.g.*, Graham, 1939; Perron, 1975), archeogastropods are generally considered to be herbivores (Yonge & Thompson, 1976). This has led several authors (Yonge, 1973; Hickman, 1984a) to imply that carnivory was not the original mode of feeding of pleurotomariids. Yonge (1973) further suggested that the change to a carnivorous diet may have been associated with the ecological shift of this family from shallow water reefs, which it inhabited during the Paleozoic and Mesozoic, to deeper water (>200 m), hard substrates by the end of the Eocene.

As members of all three Recent pleurotomariid genera have radulae with filament-tipped teeth, it would appear that spongivory in Pleurotomariidae predates the divergence of the genus *Entemnotrochus* Fischer, 1885, characterized by a deep, broad umbilicus and an anal slit extending nearly 180° back from the aperture, from the genera *Perotrochus* Fischer, 1885, and *Mikadotrochus* Lindholm, 1927, both with shallow (<90°) anal slits and without umbilici. Inclusion of the genus *Conotomaria* Cox, 1959, which is also characterized by having shells with deep anal slits and umbilici, in the same clade as *Entemnotrochus* would date this divergence, and therefore the adaptation to spongivory, prior to the Late Jurassic (Knight *et al.*, 1960). The restriction of the family

Table 1. Published reports on the contents of the alimentary system and fecal pellets of pleurotomariid gastropods.

Species	Food	Reference
Mikadotrochus beyrichi	Sponge spicules, order Poecilosclerida	Woodward, 1901:252
Mikadotrochus hirasei	Sponge spicules, orders Haplosclerida, Poecilosclerida, and Hadromerida	Arakawa *et al.*, 1978 (table 1)
Perotrochus africanus	Amorphous mass with few tiny foraminiferans	Barnard, 1963:156
Perotrochus amabilis	Sponge spicules, foraminiferans, diatoms, and algal fragments	Fretter, 1964:182
Perotrochus amabilis	Sponge spicules, foraminiferans, and diatoms	Present study
Perotrochus midas	Sponge spicules, foraminiferans, and diatoms	Present study

to bathyal depths at the time of formation of the psychrosphere, the lower, cooler layer of a two-layer ocean (Bruun, 1957; Benson, 1975) was accompanied by a considerable reduction in diversity, compared to Paleozoic and Mesozoic fauna (Woodward, 1885).

Many sponges contain secondary metabolites that are toxic (Green, 1977; Bakus & Thun, 1979). Nevertheless, mollusks, echinoderms, fishes, and marine turtles are natural predators of sponges, with nudibranchs being among the most species-specific spongivores (Sara & Vacelet, 1973). *Halichondria okadai* (Kadota, 1922), the preferred prey of several species of nudibranchs, for example, contains potent cytotoxic, antifungal, and tumor promoting compounds (Tachibana *et al.*, 1981; Fujiki *et al.*, 1987). *Strongylophora hartmani*, the sponge species eaten by *Perotrochus midas*, contains puupehenone, a cytotoxic compound (Komoto *et al.*, 1987). It is possible that incorporation of diet-derived toxic metabolites may confer some protection from predators upon pleurotomariids, but this hypothesis remains to be tested.

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A New Species of *Macrarene* (Turbinidae: Liotiinae) from Brazil

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ABSTRACT

The new species *Macrarene digitata* from the northeast Bra-
zilian coast represents the first record of this principally eastern
Pacific genus in the western Atlantic. The species had previ-
ously been known from juvenile specimens reported as *Liotia
admirabilis* E. A. Smith, the holotype of which is not a member
of the subfamily Liotiinae.

INTRODUCTION

The species here described was first recognized as a mem-
ber of the Brazilian fauna by Rios (1975, 1985), who
referred it to *Liotia admirabilis* E. A. Smith, 1890. That
species was described from the oceanic island of Saint
Helena. According to the original description, Smith's
species has a maximum dimension of 1⅓ mm. The 15
syntypes were examined at the British Museum (Natural
History) (catalogue numbers 1889.10.1.1554–68) by the
senior author in 1984 and found to be similar (although
not clearly referable) to the skeneiform genus *Parviturbo*
Pilsbry & McGinty, 1945, which is not a member of the
Liotiinae.

The Brazilian species was clearly undescribed, but its
true generic affinity was not readily apparent because
the specimens available to Rios, which have been ex-
amined by McLean (figure 2), were not mature and the
expression of the mature lip was impossible to determine.
More recently, two larger specimens have come to light
and it can now be maintained that the species has the
characters of the genus *Macrarene* Hertlein & Strong,
1951.

Abbreviations for institutions are as follows: LACM,
Los Angeles County Museum of Natural History; MORG,
Museu Oceanografico, Universidade do Rio Grande, R.S.,
IBUFRJ, Instituto de Biologia, Universidade Federal do
Rio de Janeiro.

SYSTEMATICS

Family **Turbinidae** Rafinesque, 1815

Subfamily **Liotiinae** H. & A. Adams, 1854

Shells of the subfamily are characterized by turbiniform
to discoidal profiles, nacreous interiors, fine lamellar
sculpture, intritacalx (calcified periostracum) in most
genera, circular apertures, and multispiral opercula with
calcareous beads. Radula like that of members of other
turbinid subfamilies.

Although previously treated by most authors as a full
family, the Liotiinae have recently been ranked as a
subfamily of Turbinidae by McLean (1987).

Genus *Macrarene* Hertlein & Strong, 1951

Type species (original designation): *Liotia californica*
Dall, 1908. Recent, off Baja California, Mexico.

Macrarene species are characterized by turbinate white
shells, broad umbilici, and presence of axial ribs and
spiral cords that form spines at their intersections. Spac-
ing of the axial ribs increases in the final whorl. In some
species the ribs then become more closely spaced in the
final quarter whorl. The final lip is not thickened at
maturity.

Some *Macrarene* species reach relatively large sizes.
The genus differs from *Arene* in lacking shell pigmen-
tation and in having the spacing of the axial sculpture
increasingly separated as the shell matures. The white-
shelled genus *Liotia* is smaller and retains tight spacing
of the axial sculpture.

The white-shelled, new world Liotiine genera *Mac-
rarene*, *Liotia*, and *Cyclostrema* differ as a group from
those of the Indo-Pacific and Australasian regions in lack-
ing the thickened mature lips that characterize the gen-
era *Bathyliotina* Habe, 1961, *Liotina* Fischer, 1885,
Dentarene Iredale, 1929, and *Austroliotia* Cotton, 1948.
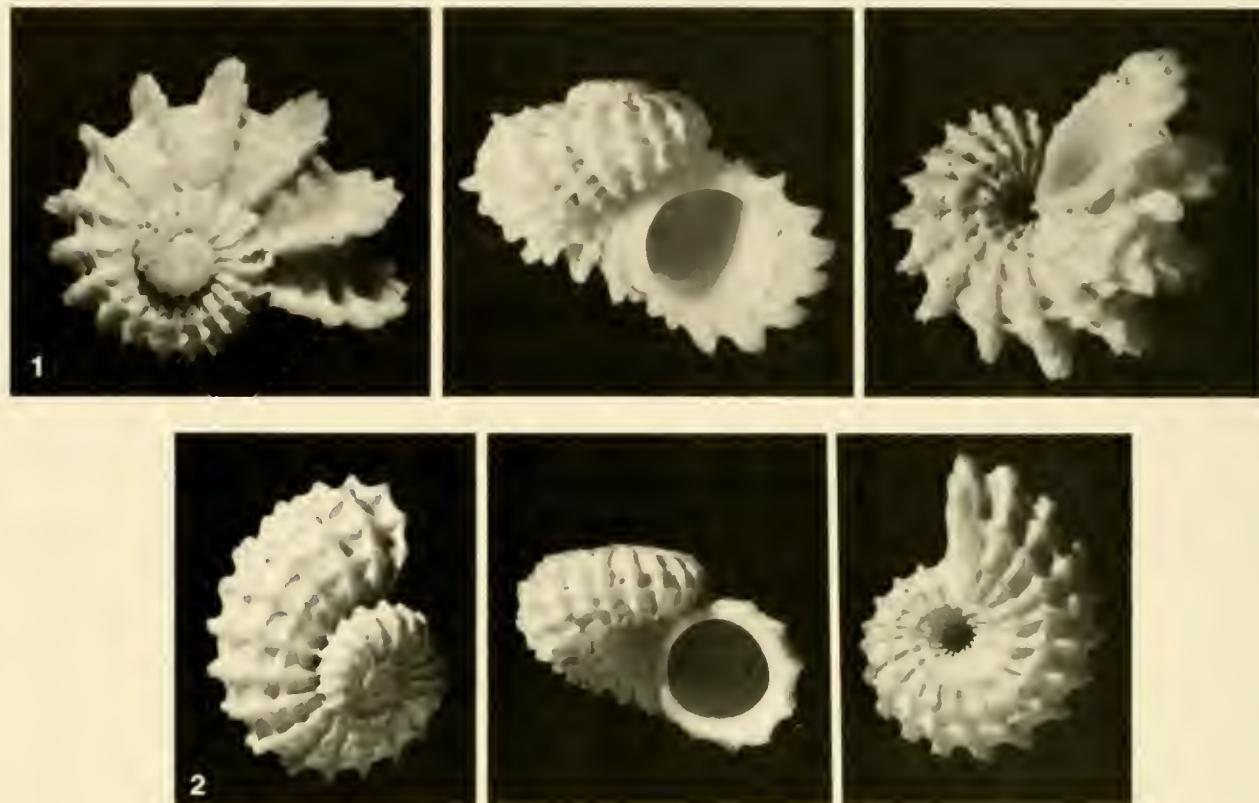
Figures 1, 2. *Macrarene digitata* new species. **1.** Holotype, IBUFRJ 1562. × 7.1. **2.** Immature specimen, MORG 18.359. × 10.0.

For further remarks on the Indo-Pacific group see McLean (1988).

There are six previously described species of *Macrarene*: *M. californica* (Dall, 1908), *M. cookeana* (Dall, 1908), *M. diegensis* McLean, 1964 (Pliocene); *M. farallonensis* (A. G. Smith, 1952), *M. lepidotera* McLean, 1970, and *M. spectabilospina* Shasky, 1970. All occur offshore in the tropical to temperate eastern Pacific.

Macrarene digitata new species
(figures 1, 2)

Description: Shell small for genus, turbinate, white, interior weakly nacreous, maximum diameter 6.7 mm, whorls 3.5, aperture only slightly oblique, final lip not thickened. Whorls circular in outline; final whorl in contact with previous whorl at tips of axial ribs. Shell surface marked by microscopic lamellar growth increments; intritacalx present. Protoconch diameter about 200 μm. Suture deeply impressed, first and second whorls rising above protoconch, third whorl descending, resulting in flat-topped profile for early whorls. First teleoconch whorl nearly smooth (except for fine lamellar sculpture), second with about 20 strong axial ribs and nine, nearly equal spiral cords defining deep, rectangular pits. Intersections of axial and spiral sculpture produce sharply projecting spines that are slightly upturned adapically. Spiral cords of final whorl increasing to 12; axial ribs decreasing to 15. Spines produced on final whorl by interaction of spiral

and axial sculpture; spines with weblike interconnections. Axial ribs narrow across umbilical wall, forming single descending row of sharp-pointed projections along innermost spiral cord. Operculum and radula unknown.

Type locality: Off northeast coast of Brazil (03°59′N, 49°35′W), 100 m, Brazilian Naval Research Vessel *Almirante Saldanha*, station 1913, May 6, 1968, 1 specimen.

Type material: Holotype (figure 1), IBUFRJ 1562. Height 5.0 mm, diameter 6.7 mm. The holotype is a dead collected specimen in good condition. Paratype, LACM 2377, off Cabo San Roque, Rio Grande do Norte, Brazil (04°30′S, 50°03′W), 146 m, Brazilian Naval Research Vessel *Almirante Saldanha*, station 1921, May 8, 1968 (height 4.3 mm, diameter 6.6 mm). The paratype agrees with the holotype in size and sculptural details but is in subfossil condition with attached sedimentary deposits on the base.

Referred material: MORG 18.359, 2 immature specimens [height 2.7, diameter 4.3 mm (figure 2); height 1.5, diameter 2.6] from Paripueira, Alagoas, Brazil, in beach drift collected by P. S. Cardoso, December, 1964; MORG 20.620, 2 immature specimens (height 2.1, diameter 3.7 mm; height 2.4, diameter 3.6 mm), Fernando de Noronha Island, 6 m, collected by L. Barcellos, January, 1979.

Etymology: From the Latin *digitatus*, having fingers.

Remarks: *Macrarene digitata* is the smallest species of the genus described to date. However, it is not certain that the holotype is mature. Although this genus does not form a thickened lip, maturity in other members of the genus is indicated by closer spacing of the axial elements in the final quarter whorl of growth, as indicated in the original illustration of *M. spectabilospina* of Shasky (1970: fig. 2). The absence of such closer spacing of the axial element suggests that a quarter whorl of additional growth (and a substantial increase in diameter) is possible for *M. digitata*.

Macrarene digitata is unique in the genus in having all elements of the spiral sculpture of similar strength, rather than having a strongly projecting peripheral carination. Such a sculptural distinction is not regarded as a generic level character because generic characters in the Liotiinae are more reliably based on apertural morphology, particularly the structure of the final lip.

The most characteristic feature of this species is the fingerlike aspect of the projecting spines. It cannot easily be confused with any other member of the Liotiinae.

ACKNOWLEDGEMENTS

We are grateful to Prof. E. C. Rios for the loan of the referred material of this species.

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Nerita fortidentata, a New Gastropod from the Neogene of Panamá, with Comments on the Fossil Record of Nerita in Tropical America

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ABSTRACT

Nerita fortidentata new species is described from the Neogene of Bocas del Toro, Panamá. It is most closely related to the Recent Caribbean *N. fulgurans* Gmelin, 1791. The fossil record and biogeography of tropical American *Nerita* are reviewed. At least two lineages of *Nerita* present in tropical America during the Tertiary have become restricted in the Recent fauna to the Indo-West-Pacific region.

INTRODUCTION

Neritid gastropods are prominent members of tropical rocky intertidal communities. Because the fossilization potential of these animals is poor, little is known about the historical development of the genus *Nerita* Linnaeus, 1758. It was, therefore, of considerable interest to find an excellently preserved specimen of an apparently hitherto unrecognized species from the Neogene of tropical America. Here we describe the new species and review briefly some biogeographically interesting aspects of the history of the genus *Nerita* in tropical America.

METHODS

Species of *Nerita* are distinguished conchologically by characters of shape, apertural dentition, external sculpture, form and sculpture of the parietal callus, and the shape and sculpture of the calcareous operculum. Two ratios are especially helpful in describing the overall shell form of *Nerita* (Vermeij, 1973). The first is globosity, G, defined as the distance H_1 between the dorsal surface of the body whorl and the center of the parietal callus divided by the geometric mean between the shell's major diameter D_1 and minor diameter D_2: $G = H_1/(D_1D_2)^{1/2}$. The second ratio is the degree of basal excavation. The plane of the parietal callus typically lies at an angle to the horizontal when the shell lies aperture-down on a flat surface. The greater the angle, the greater is the degree of basal excavation. An approximation of the degree of basal excavation is given by the ratio $E = H_2/$ H_1, where H_2 is the distance from the horizontal plane on which the shell rests to the dorsal surface of the body whorl.

SYSTEMATIC DESCRIPTION

Class **Gastropoda**
Subclass **Prosobranchia**
Order **Neritacea**
Family **Neritidae**

Genus *Nerita* Linnaeus, 1758

Type species: *Nerita peloronta* 1758, Recent, tropical Western Atlantic.

Subgenus *Theliostyla* Mörch, 1852

Type species: *Nerita albicilla* Linnaeus, 1758, Recent, Indo-West-Pacific.

Nerita (Theliostyla) fortidentata new species
(figures 1, 2)

Diagnosis: Shell thick, moderately globose (G = 0.59), base little excavated (E = 1.10), apex of spire barely raised above rest of shell. Outer lip very thick, inner edge with 12 strong teeth; two teeth nearest spire very large and protruding, as is third tooth from abapical end of lip; columellar lip with two strong centrally placed teeth; adapical portion of parietal region with a fold of about the same size and strength as adapical tooth, which curves into aperture; sculpture consisting of 21 regularly-spaced flat-topped smooth spiral cords, which flare slightly from base to barely overhang incised interspaces about one-third the width of ribs; parietal callus small, its surface sculptured with about 10 strong ridges that bear up to 3 large granules each; holotype shows faint radial color pattern of alternating continuous and discontinuous prosocline bands of off white and grey-black; operculum unknown.

Figure 1. *Nerita fortidentata* new species, from Bocas del Toro, Panamá. Holotype, USNM 423644, height 19.7 mm. Apertural view, showing thickened outer lip and enlarged teeth on adapical portion of outer lip.

Holotype: United States National Museum number 423644. Major diameter 21.3 mm, minor diameter 16.9 mm, H_1 11.2 mm, H_2 12.3 mm, standard shell height 19.7 mm (apex abraded), standard shell diameter 19.9 mm, shell thickness at midpoint of outer lip 3.5 mm.

Type locality: Panamá, Province of Bocas del Toro, Archipelago of Bocas del Toro, Punta Robalo quadrangle, Island of Cayo Agua, eastern side about 400 meters south of Punta Nispero on the shoreline in clayey, tuffaceous, quartzose, blue-grey siltstones with dense shelly horizons. We have followed Woodring (1982) in referring to the Late Miocene–Pliocene deposits of the Bocas del Toro area as the Limónes Formation. The true relationships between the Miocene–Pliocene of Bocas del Toro with respect to the Costan Rican Limónes Formation and the Gatun Formation of the Canal Zone have not been elucidated. Laurel Bybell of the U.S.G.S. (personal communication) has assigned a preliminary age of Late Miocene to Early Pliocene to the locality from which the holotype of *N. fortidentata* was collected. This age determination is based on the presence of the calcareous nannofossils *Sphenolithus abies* Deflandre, *in* Deflandre and Fert, 1954 (last occurrence middle Pliocene), and *Discoaster brouweri* Tan, 1927 (first occurrence middle Miocene). Thomas M. Cronin, U.S.G.S. (personal communication), examined the ostracode faunas from several adjacent localities of the same formation on Cayo Agua. He noted a remarkable similarity between the ostracodes from these samples and the ostracode fauna described by van den Bold (1967) from the type Gatun Formation of the Canal Zone. On the basis of these similarities he suggests a preliminary age of Late Miocene for this fauna. Harry Dowsett, also of the U.S.G.S. (personal communication), examined the planktic foraminifera from an adjacent locality of the same formation on Cayo Agua and found an assemblage indicative of planktic zone N17–N18 (Late Miocene–Early Pliocene). The consensus at this stage, therefore, is that the beds from which *N. fortidentata* was collected are Late Miocene to Early Pliocene in age.

Figure 2. *Nerita fortidentata* new species, from Bocas del Toro, Panamá. Holotype, UNSM 423644, height 19.7 mm. Ab-apertural view.

Remarks: The new species clearly belongs to the subgenus *Theliostyla* Mörch, 1852 (type *N. albicilla* Linnaeus, 1758), which is characterized by granulate sculpture on the parietal region, a barely protruding spire, and well-developed external spiral sculpture. Among the four Recent species of this subgenus in tropical America, *N. fulgurans* Gmelin, 1791, bears the closest resemblance to *N. fortidentata*. Measurements of 17 specimens of *N. fulgurans* in the Vermeij collection from the Atlantic coasts of Panamá, Costa Rica, Venezuela, and Jamaica show that this species is less globose (G = 0.54 ± 0.020, range 0.50–0.57) and basally much more excavated (E = 1.27 ± 0.05, range 1.21–1.39) than is the new species. *Nerita funiculata* Menke, 1851, the Recent eastern Pacific cognate of *N. fulgurans*, is also less globose (G = 0.51 ± 0.04, range 0.42–0.58, based on 15 specimens in the Vermeij collection from Costa Rica, Panamá, and Ecuador) and more excavated (E = 1.28 ± 0.15, range 1.13–1.60) than is *N. fortidentata*. Both *N. fulgurans* and *N. funiculata* have weaker and more numerous denticles on the outer lip, weaker and more finely granulated ridges on the parietal region, and spiral cords that are more numerous and more variable in size on the body whorl (18–35 in *N. fulgurans*, usually more than 30 in *N. funiculata*). The spiral cords of *N. fulgurans* show a tendency to bifurcate on the body whorl, whereas no such tendency is seen in *N. fortidentata*. The three subspecies of *N. ascensionensis* Gmelin, 1791, from islands in the tropical south Atlantic (Vermeij, 1970) differ from *N. fortidentata* by having a nearly smooth parietal region and by the very weak dentition on the outer lip. The West Indian *N. tessellata* Gmelin, 1791, differs from *N. fortidentata* by having low rounded spiral cords broken irregularly by high and low areas correlating to the characteristic black and white checkered pattern found in this species, a finely granulated parietal region of relatively large extent, and a weakly denticulated outer lip (Russell, 1941).

Jung (1965) recorded *Nerita fulgurans* from the Middle Miocene and Upper Pliocene of Venezuela, but he pointed out that his specimens differed from Recent shells by having stronger apertural dentition and a less concave

(that is, less excavated) parietal region. Later Jung (1969) found a similar shell in the Late Miocene Melajo Clay Member of the Springvale Formation of Trinidad. Like the Venezuelan material, the shell from Trinidad has only 16 ribs, but instead of having 2 centrally placed columellar teeth, as in the Venezuelan material, the Trinidad specimen has one upper tooth which curves into the aperture (this upper tooth is probably equivalent to the parietal fold found on the type of *N. fortidentata*) and 2 somewhat lower denticles. Jung tentatively referred both lots to *N. exuvioides* Trechmann, 1935, a species described on the basis of one incomplete specimen from the Pliocene of Carriacou in the Grenadines. Jung (1971) redescribed this latter specimen as having only 12 ribs whose edges overhang the adjacent interspaces. Vokes (1983) clarified the status of *N. exuvioides* when she described a very strongly ribbed shell with 11 ribs from the Gatun Formation of Panamá. This specimen closely resembles the one from Carriacou and is clearly referable to *N. exuvioides*. We believe that Jung's (1965, 1969) specimens from Venezuela and Trinidad belong neither to *N. fulgurans* nor to *N. exuvioides*, but instead to our new species, *N. fortidentata*. This species appears therefore to be intermediate in sculpture between *N. exuvioides* with only 11–12 ribs and the Recent *N. fulgurans*, usually with more than 21 ribs. The relationship between *N. fortidentata* and the Late Oligocene or Early Miocene *N. tampaensis* Dall, 1892, from the Tampa Formation of Florida is unclear. *Nerita tampaensis*, whose granulated parietal region suggests placement in *Theliostyla*, is a small species with weakly developed apertural dentition and highly variable external sculpture, some shells being nearly smooth whereas others have fine spiral cords of varying sizes.

The shape of *N. fortidentata* suggests that this species inhabited the upper zones of rocky shores. *Nerita fulgurans*, its most similar living relative, is usually found in areas of reduced salinity, such as the mouths of harbors (Russell, 1941) or protected embayments. Vermeij (1973) showed that shells with low globosity, high basal excavation, weak sculpture, and relatively broad apertures with weak dentition are found in middle to lower intertidal species of *Nerita*; whereas species with a globose, little excavated, strongly sculptured shell and a small aperture bordered by strong teeth are found at higher shore levels. The latter shell form is especially characteristic of the subgenera *Cymostyla* von Martens, 1887, and *Ritena* Gray, 1858. Of the living and fossil members of the subgenus *Theliostyla*, most of which live in the middle zones of the intertidal, *N. fortidentata* most closely approaches species of *Ritena*. Other fossils collected with *N. fortidentata*, including *Oliva*, *Olivella*, *Conus*, *Natica*, *Polinices*, *Strombus*, *Phalium*, *Dentalium*, and *Corbula*, suggest a variety of different environments, implying post-mortem transport and mixing of assemblages.

BIOGEOGRAPHY OF AMERICAN *NERITA*

Among the fossil species of *Nerita* that have been described from late Eocene and younger strata in tropical America, at least two have close affinities with living Indo-West-Pacific species. *Nerita listrota* Woodring, 1973, from the late Eocene (?) Gatuncillo Formation of Panamá has a finely ribbed shell with a peripheral keel, fine teeth on the outer lip, 7 teeth on the columellar lip, and a sparsely papillate parietal region. Woodring (1973) noted the striking similarity between *N. listrota* and the recent mangrove-associated *N. planospira* Anton, 1839 (the type and only known species of the subgenus *Ilynerita* von Martens, 1887) from the tropical Indo-Pacific. He doubted that the two species were closely related, in part because *N. planospira* has 5 rather than 7 columellar denticles. We consider the similarities to be so numerous that an inference of close relationship seems warranted. If *N. listrota* belongs to the subgenus *Ilynerita*, as we believe it does, that subgenus may be added to the growing list of taxa whose distributions became restricted to the Indo-West-Pacific during the Tertiary (Vermeij, 1986). As Vokes (1983) points out, *N. (Theliostyla) exuvioides* may represent a second lineage that has become restricted (as *N. exuvia* Linnaeus, 1758) to the Indo-West-Pacific. *Nerita exuvioides* differs from the Western Pacific *N. exuvia* chiefly by having 11 instead of 14 strong overhanging spiral cords on the body whorl.

The other fossil species of *Nerita* that have been described from late Eocene and younger deposits in tropical America do not easily fit with any living members of the genus. These are *N. hadra* Woodring, 1973, from the late Eocene (?) Gatuncillo Formation of Panamá and *N. oligopleura* Dall and Ochsner, 1928, from the Pleistocene of the Galapagos. *Nerita hadra* has very fine spiral threads on the body whorl and a smooth parietal region, whereas *N. oligopleura* has 3 broad spiral ribs on the body whorl.

Although the record of *Nerita* in tropical America is very meager, the history of the genus points to multiple instances of extinction and geographical restriction. It is too early to assess the scope of these changes, but the record of *Nerita* suggests that intertidal species have been no less affected by events leading to extinction and restriction than have species from the better-sampled fossil environments of subtidal bottoms.

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A New Species of *Favartia* from the Eastern Pacific (Gastropoda: Muricidae)

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ABSTRACT

Favartia (*Murexiella*) *shaskyi* is described from Isla del Coco, Costa Rica, and compared with related species from the eastern Pacific. This species is known only from this isolated oceanic island.

INTRODUCTION

Isla del Coco (also known as Cocos Island), one of the National Parks of Costa Rica, is a small, uninhabited island situated approximately 600 kilometers south southwest of Puntarenas, Costa Rica, at 5°33′N latitude and 87°03′W longitude. Isla Cascara and Roca Sucia are two of the many islets surrounding Cocos Island. In May, 1985, Donald R. Shasky of Redlands, California, and Kirstie L. Kaiser of La Canada, California, collected five specimens of the new species described herein, at depths of 50–80 feet (15.2–24.4 m), under dead coral off these two islets. In a previous paper (D'Attilio, Myers & Shasky, et al., 1987), a new species of *Phyllonotus* Swainson, 1833, was described from the same area. Montoya (1983, 1984) published a bibliography of Cocos Island molluscan faunal studies.

SYSTEMATICS

Family **Muricidae** Rafinesque, 1815
Subfamily **Muricopsinae** Radwin & D'Attilio, 1971

Genus *Favartia* Jousseaume, 1880

**Type species:** *Murex breviculus* Sowerby, 1834, by original designation.

Subgenus *Murexiella* Clench & Pérez Farfante, 1945

Type species: *Murex hidalgoi* Crosse, 1869, by original designation.

Favartia (*Murexiella*) *shaskyi* new species
(figures 1–10)

Description: Shell (figures 1, 2) broadly fusiform, spire ⅓ shell length; protoconch of holotype eroded, protoconch of paratype 1 (figure 3) of 3½ smooth, lustrous, convex whorls, with axial buttresses arising from the teleoconch; teleoconch with 5–6 subangulate whorls; suture weakly impressed; whorls gently sloping from suture to shoulder; body whorl ⅔ shell length; aperture ovate; inner lip erect posteriorly; outer lip thin, erect, crenulate, reflecting the spiral cords; siphonal canal ⅓ shell length, broad proximally, tapering distally, with narrow ventral opening, terminally recurved, tube-like; siphonal fasciole of 3 fine distal portions of previous canals; body whorl with 6 broad varices, penultimate whorl with 8 varices; varices broader than intervarical regions; spiral sculpture of 6 cords on body whorl, all nearly equal in width, packed closely together; 2 additional cords between body whorl and siphonal canal, 2 major and 1 minor cord on canal; 2 cords per whorl on spire; shoulder of body whorl without spiral cords; all cords terminate as spines on varices (figures 4, 5), posterior spines recurved, anterior spines long, projecting ventrally; spiral cords (figures 6, 7) strongly scabrous; scales prominent, fine, white, erect, closely packed, disguising the contour of cords; cords and scales microscopically grooved, incrementally incised; adapertural sides of varices, especially last varix, completely scaled; scales arranged in 3 tiers (figure 6), with tube-like spines on tier farthest from aperture; radula (figure 8) typically muricopsine, with broad, U-shaped basal plate, and strongly projecting cusps. Paratypes 1 and 2 with only 4 postnuclear whorls; suture more strongly impressed, spire angulate.

Figures 1, 2. *Favartia* (*Murexiella*) *shaskyi* new species. **1.** Holotype, USNM 860012, Isla Cascara, Cocos Island, Costa Rica, under dead coral slab, in 24.4 m, 23.0 mm long. **2.** Paratype 1, SDNHM 91873, Roca Sucia, Cocos Island, Costa Rica, under dead coral slab, in 24.4 m, 14.0 mm long.
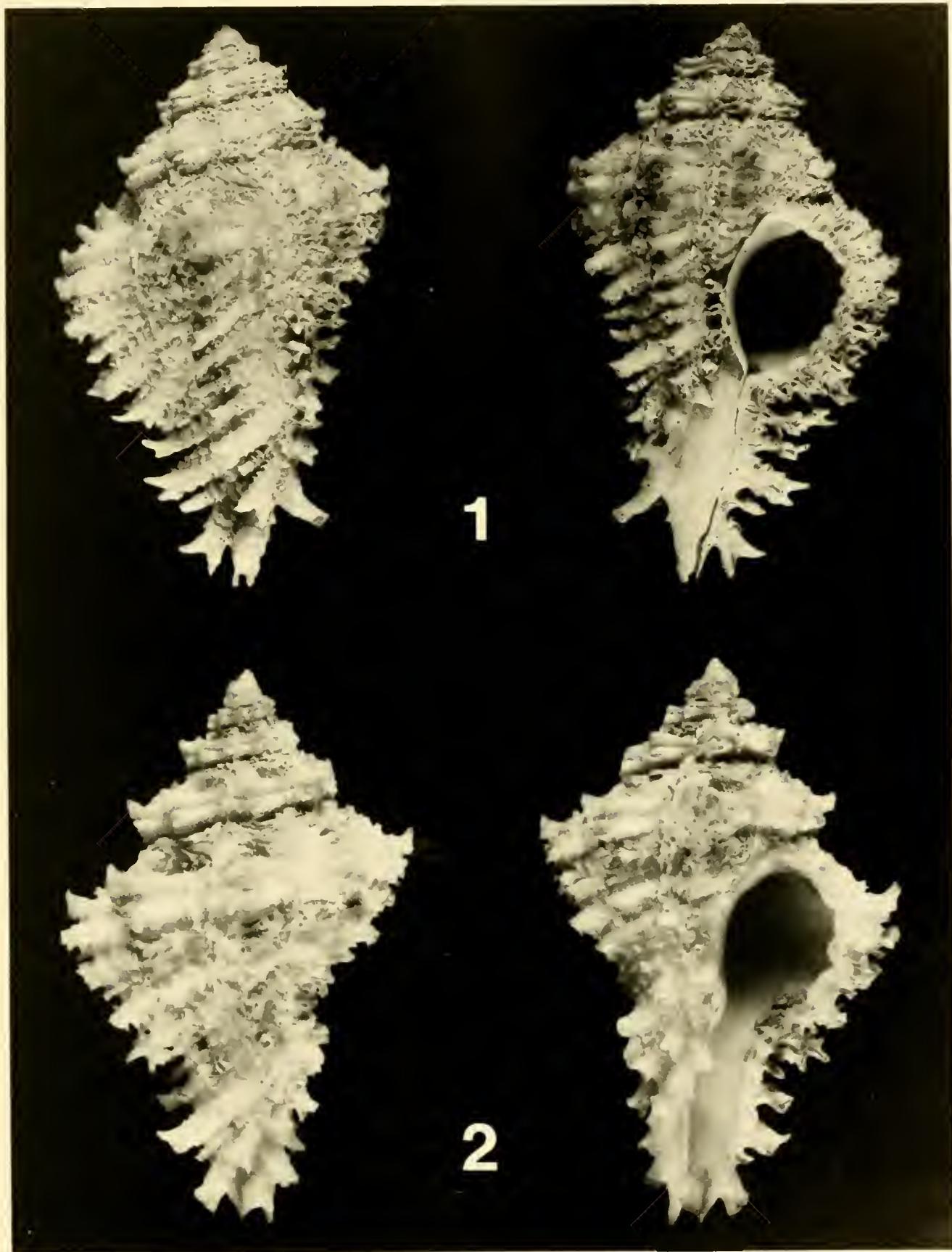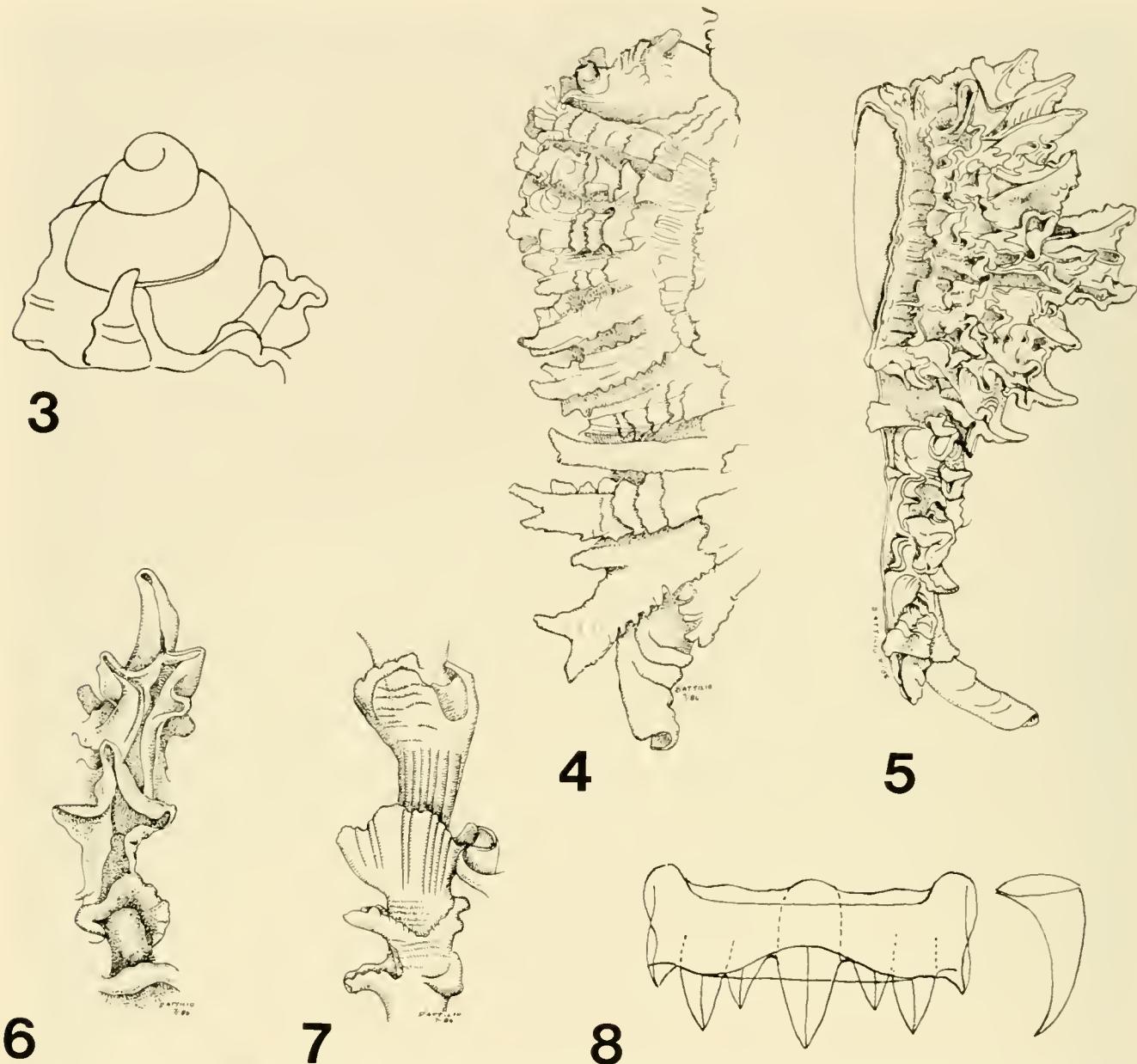
Figures 3–7. *Favartia (Murexiella) shaskyi* new species, details of shell sculpture. **3.** Protoconch of paratype 1. **4, 5.** Adapertural (4) and abapertural (5) views of last varix of holotype. **6, 7.** Microsculpture along adapertural (6) and abapertural (7) surfaces of a spiral cord of the holotype. **Figure 8.** Rachidian and right lateral teeth from the holotype.

Color: Base color buff to tan, with diffuse darker band encircling body whorl; scales white, aperture white, siphonal canal white.

Type locality: Isla Cascara, Cocos Island, Costa Rica, under dead coral slab, in 24.4 m.

Holotype: USNM 860012 (figure 1), 23.0 mm long, 14.2 mm wide.

Paratypes: Paratype 1: SDNHM 91873 (figure 2), 14.0 mm long. Paratype 2: Collection of D. R. Shasky, 11.8 mm long, both from Roca Sucia, Cocos Island, Costa Rica, under dead coral, in 24.4 m.

Additional material examined: Two specimens, collection of K. Kaiser, 19.2 mm long, and 14.7 mm long, Isla Cascara, Cocos Island, Costa Rica, under rocks, in 15.2–24.4 m.

Etymology: We are pleased to name this species for Donald R. Shasky, M.D., who collected the three type specimens, and who generously donated the holotype and paratype 1.

DISCUSSION

This new species has a distinct morphology that easily distinguishes it from all other eastern Pacific species of

the subgenus *Murexiella*. *Favartia* (*Murexiella*) *lappa* (Broderip, 1833), a closely related species, differs in having a higher spire, biconic form, and short, stubby, non-recurved spines. *Favartia* (*Murexiella*) *vittata* (Broderip, 1833) also has a more or less biconic shape, but the body whorl is more globose, and the spines, although recurved, are short and stubby. *Favartia* (*Murexiella*) *keenae* (E. H. Vokes, 1970) has somewhat similar sculpture, a larger shell with a globose body whorl strongly constricted at the base, and a strongly impressed suture. We have carefully studied and compared the 12 additional nominal species of *Murexiella*, none of which are closely related to this new species.

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Conus baccatus G. B. Sowerby III, 1877:
A Panamic Faunal Constituent

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ABSTRACT

Specimens of a small species of *Conus* recently received from Golfo de Chiriquí, República de Panamá, are confirmed to be referable to *Conus baccatus* Sowerby, 1877, a species originally described from an unknown locality. The provenance and identity of this taxon had remained uncertain for more than 100 years until Röckel (1985a) compared two specimens from Pacific Panama in his collection with the holotype of *Conus baccatus* and determined the specimens to be conspecific. We agree with Röckel's conclusion that this species has been confused in the past with the pustulate form of the west American *Conus perplexus* Sowerby, 1857, which is a somewhat similar, but distinct species. For *Conus perplexus*, a lectotype is selected and the type locality is restricted to the Golfo de Panamá. For *Conus baccatus*, the Golfo de Chiriquí is designated the type locality.

INTRODUCTION

In 1877, G. B. Sowerby III briefly described and illustrated in color *Conus baccatus* from an unknown locality. Apparently based on a single specimen in the collection of Dr. Prevost of Alençon, France, the figured specimen later was owned by J. C. Melvill (Sowerby, 1887:251) and subsequently by J. R. Le B. Tomlin (1937:217). The vast Melvill-Tomlin Collection eventually was deposited, along with this type, in the National Museum of Wales, Cardiff. Coomans *et al.* (1982:4) examined the holotype and provisionally accepted *Conus baccatus* as a valid species. They also rejected the questionable placement by Walls (1979:726) of this taxon in the synonymy of *C. mindanus* Hwass *in* Bruguière, 1792, from the western

Atlantic. Vink (1984:356) subsequently noted certain similarities of the holotype of *C. baccatus* with *C. selenae* Van Mol, Tursch, and Kempf, 1967, a Brazilian taxon which we consider referable to the *C. jaspideus* Gmelin, 1791, species complex.

Through the generosity of Carol Skoglund and Robert Koch, we have examined a series of well-preserved specimens from Golfo de Chiriquí, Panama that are referable to *Conus baccatus*. Our findings confirm Röckel's (1985a: 29) conclusion that this taxon is a valid Pacific Panamic species, which for many years has been masquerading in collections as a pustulose form of *Conus perplexus* Sowerby, 1857.

A specimen apparently referable to *C. baccatus* was illustrated by Kiener (1846:56, 57, pl. 83, fig. 2) as "*Conus albomaculatus*, Reeve", in reference to Sow.[erby] (1833, *Conus* fig. 2, which was named *C. bicolor* by Sowerby in 1833 and renamed *C. albomaculatus* by Sowerby in 1841). Kiener's figured specimen, measuring 22 mm in height, was attributed to the Dupont Collection from an unknown locality. This specimen cannot be located in the Muséum National d'Histoire Naturelle, Paris, and the fate of the Dupont collection is not known (P. Bouchet, *in litt.*, March 4, 1987). Reeve (1849:3) considered Kiener's illustrations to represent the western Atlantic species *C. mindanus* Hwass *in* Bruguière, 1792. He also stated that "*C. albimaculatus* [sic] [Sowerby] has more resemblance with very young [pustulose] specimens of *C. lithoglyphus* [sic] [Hwass *in* Bruguière, 1792]", a conclusion accepted by Coomans *et al.* (1979:97) and Röckel (1985b, nr. 22). Sowerby's figured specimen of *C. albomaculatus* has not been located. It is not in the British Museum (Natural History) (K. M. Way, *in litt.*, May 11,

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Figures 1–7. *Conus baccatus* Sowerby, 1877. **1, 2.** Holotype, NMW no. 1955.158.29; × 2 (courtesy of R. M. Filmer). **3, 4.** Off Isla Coiba, Panama, AMNH no. 221871a; × 2. **5.** Off Isla Parida, Panama, AMNH no. 173698a; × 5. **6, 7.** Off Isla Coiba, Panama, AMNH no. 221871; × 2. **Figures 8–16.** *Conus perplexus* Sowerby, 1857. **8, 9.** Lectotype, BM(NH) no. 1978118; × 2. **10.** Playa de los Angeles, Bahía Tenacatita, Jalisco, Mexico, dredged, mud bottom, Aug., 1975, AMNH no. 221873a, *ex* C. and P. Skoglund; × 5. **11, 12.** Paralectotype, BM(NH) no. 1978118a; × 2. **13, 14.** Paralectotype, BM(NH) no. 1978118b; × 2. **15, 16.** "West Panama" (note the distorted spire), AMNH no. 212547; × 2. **Figures 17, 18.** *Conus puncticulatus* form *papillosus* Kiener, 1849, Cartagena, Colombia, beach, 1977, *ex* J. M. Bijur Coll., AMNH no. 225979; × 2. **Figure 19.** *Conus yemanjae* Van Mol *et al.*, 1967, paratype, pl. 8, fig. 1b, Fortaleza (Ceara), Brazil, *ex pisce*; × 2.
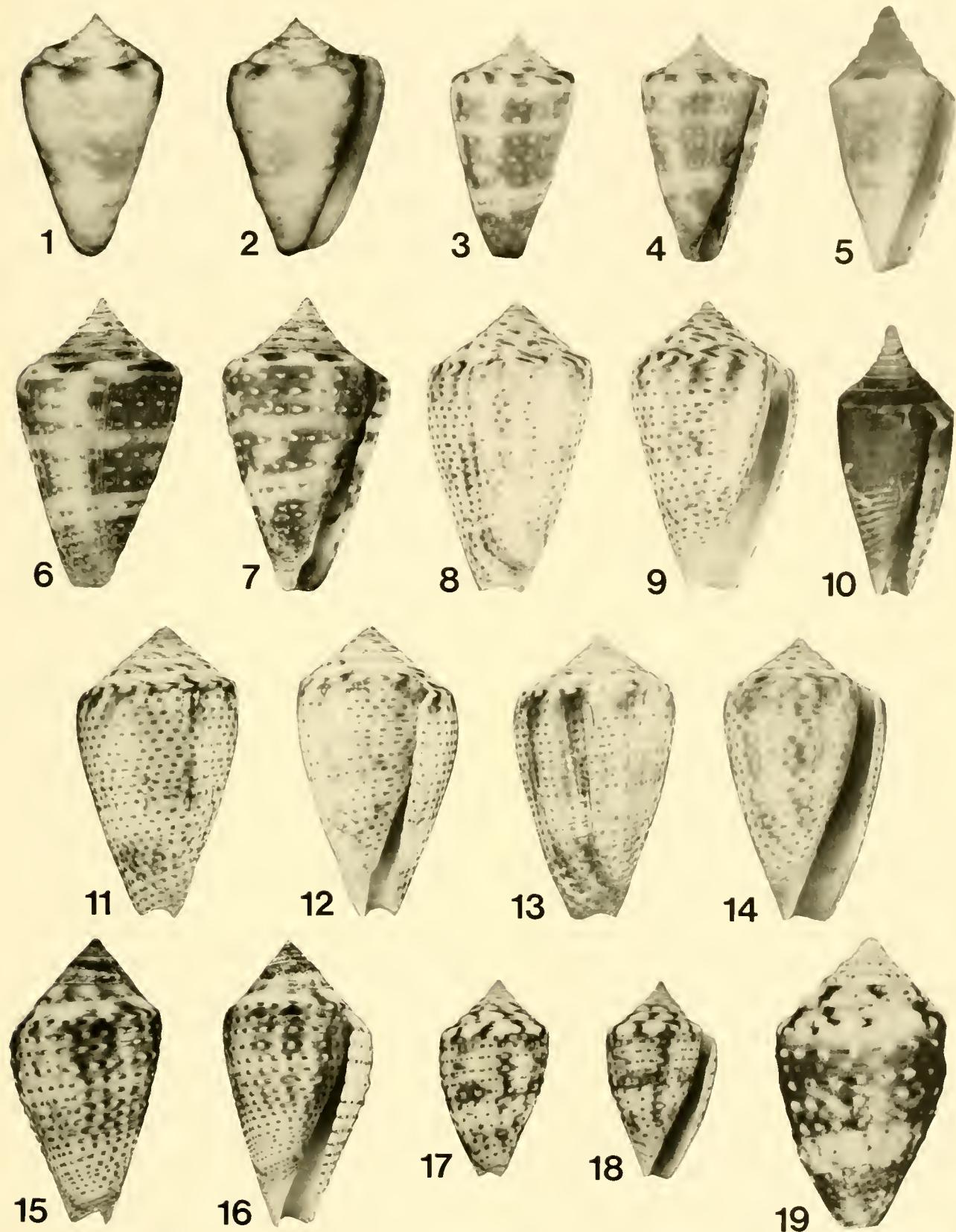
1987) nor is it in the National Museum of Wales (A. Trew, *in litt.*, May, 1987). Therefore, the taxonomic status of *C. albomaculatus* Sowerby, 1841, cannot be determined from the available data.

Although *C. baccatus* was not formally named by Sowerby III until 1877, specimens were apparently available in European collections by the mid-19th century, as suggested by Kiener's figured specimen from the Dupont collection. There is also a specimen of *C. baccatus* labeled "Panama" in the F. A. Constable Collection (AMNH 47740), which dates from the latter part of the 19th century and was received by the American Museum of Natural History from the estate of Louise Constable in 1929.

Abbreviations for institutions used in text; AMNH = American Museum of Natural History; BM(NH) = British Museum (Natural History); Los Angeles County Museum of Natural History = LACMNH; NMW = National Museum of Wales.

SYSTEMATIC ACCOUNT

Conus baccatus Sowerby, 1877
(figures 1–7)

? "*Conus albomaculatus*, Reeve", Kiener, 1846:56, 57, pl. 83, fig. 2 (apertural and dorsal views; as "*Conus albimaculatus* [*sic*] Sow.[erby]"), from unknown locality, Dupont collection. Not *C. bicolor* Sowerby, 1833: pt. 24, fig. 2, renamed without explanation *C. albomaculatus* Sowerby, 1841.

Conus baccatus Sowerby, 1877:753, 754, pl. 75, fig. 5, from unknown locality; Tryon, 1883: ser. 1, vol. 6, p. 22, pl. 6, fig. 92 [copy of original fig.], "Habitat unknown"; Sowerby, 1887: vol. 5, p. 251, *Conus* pl. 29, fig. 660 [copy of original fig.], "Habitat unknown, Coll. Melvill"; Tomlin, 1937:217, "Hab. ?, Type in coll. Tomlin"; Coomans *et al.*, 1982:4, fig. 197, apertural and dorsal views of the holotype; Vink, 1984:354–358, pl. 20, fig. 1, dorsal view of holotype; Röckel, 1985a:29, dorsal view of holotype and dorsal and apertural views of two recently collected specimens from "Perida Island", Pacific Panama (figured in color).

Original description (in part): "Shell short, rather swollen, very minutely decussated, with regular rows of conspicuous granules, whitish, with large orange blotches arranged in three bands; spire acute, short, whorls concave, nearly smooth, last whorl biangulated. . . . Apart from its somewhat stunted form, the delicacy of its markings and rows of gem-like granules, it is remarkable for the double angle at the top of the body whorl. Long. 23, lat. maj. 15 mill." [Holotype actually measures 22.2 by 14.2 mm.]

Type depository: Holotype in the National Museum of Wales, no. 1955.158.29, *fide* Trew (1982:3); here illustrated (figures 1, 2).

Type locality: Off Isla Parida, Golfo de Chiriquí, República de Panamá, here designated.

Range: Known only from Pacific Panama.

Material examined: AMNH Collection: From Golfo de Chiriquí, Pacific Panama: 6 specimens, no. 173698 and 8 specimens, no. 211778, off Isla Parida (8°05′N, 82°20′W),

in 5.5–9 m, sand bottom, May, 1972, *ex* R. E. Hubert; 2 specimens, no. 210849, off Isla Parida, sand, in 5.5 m, March, 1974, *ex* R. E. Hubert; 3 specimens, no. 225981, off Isla de Canal de Afuera, in 55 m, *ex* J. Ernest; 2 specimens, no. 221871, off Isla Coiba, in 24–40 m, March 28, 1986, *ex* C. and P. Skoglund; 2 specimens, no. 221872, off S.E. Isla Rancheria, in 2–7.5 m, March 27, 1986, *ex* C. and P. Skoglund; 2 specimens, no. 223269, off Isla Rancheria (7°38′N, 81°44′W), in 3–9 m, coral sand and debris bottom, February 24, 1987, *ex* R. Koch. From "Panama": 1 specimen, no. 47740, *ex* F. A. Constable Coll.; 3 specimens, no. 201566, *ex* T. H. and V. B. Munyan Coll.

Remarks: Specimens of *Conus baccatus* superficially resemble small examples of the pustulose form of *Conus perplexus*. There are several discrete differences in shell morphology which serve to distinguish the two taxa. 1, Nuclear whorls: In *C. baccatus*, 1½ whorls, nucleus short, terminating in a broad, well-defined mammillated process. In *C. perplexus*, 2½ whorls, nucleus elongate, narrow, terminating in a needle-like projection (*cf.* figure 5 with figure 10). 2, Shoulder margin of body whorl: In *C. baccatus*, oblique, twofold-angled (*i.e.*, biangulated). In *C. perplexus*, monoangulated (*cf.* figures 6, 7 with figures 8, 9). 3, Spiral granulations: In *C. baccatus*, rows of pustules more widely spaced, some rows weakly developed. In *C. perplexus*, rows consistently spaced, nearly uniformly developed (*cf.* figures 6, 7 with figures 15, 16). 4, Color pattern: In *C. baccatus*, spiral bands of broken blotches, orange in faded specimens, reddish-brown in fresh specimens. In *C. perplexus*, narrow spiral lines with dark brown dots (*cf.* figures 1, 2 and 3, 4 with figures 8, 9). Additionally, the periostracum in *C. baccatus* is yellowish tan, whereas in *C. perplexus* it is a brownish tan.

The largest specimen of *C. baccatus* examined (AMNH 221871a; figures 6, 7) is 26.9 mm in height, compared to a maximum of 37.8 mm for *C. perplexus* (AMNH 206684) from Isla Cébaco, Golfo de Montijo, Panama. Hanna (1963:39) reports a specimen of the latter taxon from Isla San José, Golfo de Panamá, with a height of 41.5 mm. Both of these taxa have shells with a distinct posterior notch on the lip (*cf.* figure 5 with figure 10), whereas *C. ximenes* Gray, 1839, *C. mahogani* Reeve, 1843, and *C. tornatus* Sowerby, 1833, which also have been confused with *C. perplexus*, have a narrow anal notch (see Wolfson, 1962: figs. 6a–d; Tucker 1985: fig. c; and Chaney, 1987: figs. 2, 3). All of these nominal species have populations sympatric with those of *C. baccatus*, which is known only from Pacific Panamic waters. *Conus perplexus*, with which *C. baccatus* is most likely to be confused, ranges from the northern part of the Gulf of California, south to Mancora, Peru, 4°05′S, 81°03.5′W (LACMNH no. 70-101). Specimens of *C. perplexus* in which the interrupted spiral lines of brown dashes or dots are raised into prominent pustules are more commonly found in the southern populations, from Panama southward to Peru (figures 15, 16). A similar pustulose form also occurs in populations of the western Atlantic *C. puncticulatus* Hwass *in* Bruguière, 1792, which is a twin

species of *C. perplexus*. This form was named *C. pa-pillosus* Kiener, 1849 (figures 17, 18).

On the basis of shell morphology, *C. baccatus* appears to be most closely related to members of the western Atlantic *C. jaspideus* species complex, especially the pustulose, short-spired Brazilian forms which were given the names *C. yemanjae* (figure 19) and *C. selenae* by Van Mol *et al.* (1967: pl. 8); also figured by Vink (1984: pl. 20).

Conus perplexus Sowerby (1857:20, 1858: pl. 200, fig. 324) was briefly described in Latin, followed by the comment: "This shell perplexes me, because there is a variety of *C. puncticulatus* [Hwass *in* Bruguière, 1792, a Caribbean twin species] which it nearly resembles. This, however, is quite smooth, and more angular". A single specimen was figured by Sowerby in a dorsal view, with the statement: "Gulf of California, West Columbia [*sic*], Cum.[ing]". Tomlin (1937:290) recorded the presence of three "types" in the British Museum (Naural History), which were kindly loaned to us by Ms. K. M. Way [BM(NH) 1978118, here illustrated, figures 8, 9, 11–14]. The original labels confirm these specimens as syntypes, although none of them can be referred with certainty to Sowerby's figured specimen. The drawing may represent a composite. The three syntypes are somewhat faded, but are otherwise well-preserved. We have selected as the lectotype (figures 8, 9) the syntype that most closely resembles the original figure. The lectotype is slightly larger in height (26.8 *vs.* 26.1 mm) than the specimen depicted in the original illustration.

The original labels accompanying the syntype lot of *Conus perplexus* list the Gulf of California and West Columbia [*sic*], which are the same localities cited by Sowerby (1858, caption to *Conus*, pl. 14). Hugh Cuming is not believed to have collected in Mexican waters on his voyage to the west coast of South America, 1828–30. He is known, however, to have made extensive collections in the "Gulf of Panama, the Pearl Islands, and the Gulf of Chiriqui", as well as visits to Costa Rica, Nicaragua, and Honduras (Dance, 1986:114). We here restrict the type locality of *C. perplexus* to the Golfo de Panamá, as the Isthmus of Panama was part of Colombia at that time.

In summary, *Conus baccatus* G. B. Sowerby III, 1877, is recognized as a Panamic faunal constituent and as a twin species of *C. jaspideus* Gmelin, 1791, from the western Atlantic, especially the pustulose form named *C. yemanjae* Van Mol *et al.*, 1967. *Conus baccatus* is compared with pustulose specimens of the sympatric *C. perplexus* G. B. Sowerby II, 1857, with which it has been confused, as well as with pustulose specimens of *C. puncticulatus* Hwass *in* Bruguière, 1792, a Caribbean twin species of *C. perplexus*. A lectotype is selected and the type locality is restricted for *C. perplexus*. A type locality is designated for *C. baccatus*.

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References to Molluscan Taxa Introduced by Linnaeus in the *Systema Naturae* (1758, 1767)

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ABSTRACT

Bibliographic documentation is provided for the more than 90 published resources utilized by Linnaeus as citations for mollusks in the 10th and 12th editions of his *Systema Naturae*.

INTRODUCTION

Linnaeus's 10th edition of the *Systema Naturae* of 1758 is the cornerstone of our system of binominal nomenclature in zoology. Many species of mollusks were described therein, and these have been the subject of individual investigations such as revisions of particular taxa as well as studies of the specimens themselves (Hanley, 1855; Dodge, 1952–59; Dance, 1967).

Linnaeus also attempted to apply the binominal method to the references that accompanied his treatment of the species. If he cited a reference that previously mentioned or figured the species under discussion, he usually gave an abbreviated citation, which frequently embodied a shortened name of the author and that of the individual work. Many of these are readily apparent to someone with a knowledge of the pre-Linnaean literature; thus, "Gault. test." may be easily recognized as being a reference to Gaultieri's *Index Testarum Conchyliorum* of 1742; others are more enigmatic.

Some years ago I thought that it might be interesting to decipher these puzzling references in Linnaeus's *Systema*, both the 10th (1758) and 12th (1767) editions (the 11th is a reprint of the 10th), much like Wheeler (1979) has done for fishes. However, in correspondence with the late Professor A. Myra Keen, I found that both she and Dr. S. S. Berry also had an interest in this problem. Professor Keen sent me a short draft of some 30 titles that she had connected with Linnaeus's abbreviations, and I supplied her with several that she had been unable to find. Eventually, she published a narrative account of certain authors whom Linnaeus had cited (see Keen, 1983a,b). In these papers, she noted that Linnaeus used about 40 different references in his sections on mollusks. However, when the different citations are tallied for both soft bodied and shelled mollusks [including therefore Linnaeus's categories with their genera, Vermes: Intes-

tina: *Teredo*; Vermes: Mollusca: *Clio*, *Limax*, *Doris*, *Tethys*, *Scyllaea*, and *Sepia*; and Vermes: Testacea: (all genera with the exception of *Lepas* and *Serpula* though references to the two molluscan *Serpula* are included)], the total exceeds 90. Dance (1967) also provided a short list of volumes personally owned by Linnaeus which were utilized in various editions of the *Systema*.

Unknown to any of us were the studies of Professor John L. Heller, Emeritus, of the Department of Classics of the University of Illinois on various botanical works of Linnaeus (see Heller, 1983, for a collection of these articles). He provided extensive bibliographic references to similarly abbreviated citations by Linnaeus in some of his botanical works such as the *Species Plantarum* and the *Hortus Cliffortianus*. He also explicated certain particularly equivocal abbreviations used by Linnaeus in referring to various insects (Heller, 1961) and planned to finish a complete bibliographical guide to zoological works cited by Linnaeus under the proposed title *Bibliotheca Zoologica Linnaeana* (Heller, 1968, 1979, 1983); this work is currently in press (Heller, personal communication) but will contain more than a malacologist need know.

Although I am separately preparing a more extensive treatment of the pre-Linnaean malacological citations including comments on subsequent editions, translations into other languages as well as annotations of the holdings of the Harvard College Library system (Boss, in preparation), I present below the bibliographic abbreviations utilized by Linnaeus in the *Systema Naturae* (1758, 1767) and the full citation for each reference. Of all the references, only one remains undeciphered: Linnaeus (1758: 708, 1767:1161) referred to "Tessin. epist. 1 n. 28 *Cymbium*" under *Argonauta argo*. This is presumed to have been a letter of Count Carl Gustaf Tessin, on whose collection Linnaeus worked. Despite a thorough checking of apposite sources (*i.e.*, items in the Literature Cited as well as subsequent editions of the *Systema* and several classical cephalopod authorities such as Chemnitz, Keferstein, Conrad, Naef, Robson, Tryon, and Férussac-Orbigny), this reference could not be located.

There are several bibliographic sources for pre-Linnaean works, and sometimes there are discrepancies in

citations of the sources. These may arise due to different bibliographic methods, through error, or due to the variability in the copies of pre-Linnaean works, which were not always issued in uniform copies. I have relied principally on the *Catalogue of the Books ... British Museum ...*, Soulsby (1933), Engelmann (1846), Heimann (1957), Nissen (1969), and the resources of various Harvard libraries. The birth and death dates of authors have been included, mainly as listed in the British Museum Catalogue; these do not always concur with such dates given by other authors, principally Dance (1986) or Nissen (1969). I have utilized my own method of punctuation and have spelled out such words as "engraved" and "portraits" when describing the texts; I have followed standard procedure for the usage of brackets, etc., as noted in the *Catalogue of the Books ... British Museum*. Further, the names of publishers or printers were added when I knew them. With few exceptions, which are listed as "not seen", examination of the original publication was possible.

ABBREVIATED CITATIONS UTILIZED BY LINNAEUS FOR MOLLUSKS

Act. angl. 301, p. 2051 (see Breyn, 1705)
Act. helv. 4. p. 212, t.9, f.21, 22 (see Hofer, 1760)
Act. helv. 5. p. 283, n.4, t.3, f.25, 26 or n.5 t.3 f. 27, 28 (see Schlotterbeccius, 1762)
Act. paris. 1710, p. 463 (see Réaumur, 1710)
Act. paris. 1711, t.3, f.4,5 (see Réaumur, 1711a)
Act. paris. 1711, p. 199, t.6, f.5.7. or 9 (see Réaumur, 1711b)
Act. paris. 1712, p. 163 (see Réaumur, 1712)
Act. Petropol. 7, p. 321, t.11, 12 (see Koelreuter, 1761)
Act. Upsal. 2. p. 560, t.152, f.4. idem or f.a. (see Bromell, 1729)
Adans. sen. or seneg. (see Adanson, 1757)
Aldr. exs. or exsang. or exangu. (see Aldrovandi, 1606)
Aldr. ins. (see Aldrovandi, 1602)
Amoen. acad. (see Amoenitates Academiae)
Amoen. acad. 1, p.325 (see Balk, 1746)
Amoen. acad. 3: 256 (see Odhelius, 1754)
Argenv. conch. (see Dezallier d'Argenville, 1742)
Barr. ic. or rar. or Barrel. icon. or rar. (see Barrelierus, 1714)
Baster subs. (see Baster, 1759–65)
Bell. aqu. or aquat. or Bellon. aqu. (see Belon, 1553)
Blank. ins. (see Blankaart, 1688)
Bocc. observ. (see Boccone, 1674)
Bohads. mar. (see Bohadsch, 1761)
Bonan. kirch. (see Buonanni, 1709)
Bonan. recr. or recreat. or Bonann. recr. (see Buonanni, 1681, 1684)
Brad. natur. or Bradl. nat. or Bradl. natur. (see Bradley, 1721)
Breyn. polyth. (see Breynius, 1732)
Brown. jam. (see Browne, 1756)
Brueckm. cent. 2 epist. (see Brueckmann, 1743)
Calceol. mus. (see Cerutus and Chiocco, 1622)

Chin. Lagerstr. (see Odhelius, 1754)
Column. aqu. or aquat. (see Colonna, 1606)
Column. phytob. (see Colonna, 1592)
Column. purp. (see Colonna, 1616)
Crew. mus. (see Grew, 1681)
E.N.C. (see Francus de Frankenau, 1727)
Edw. av. (see Edwards, 1758–64)
Ellis cor. or corall. (see Ellis, 1755)
En. svec. (see Linnaeus, 1746)
Faun. svec. or Fn. svec. (see Linnaeus, 1746)
Frisch ins. (see Frisch, 1730)
Gesn. aqu. or aquat. (see Gesner, 1551–87)
Ginam. adr. (see Ginnani, 1755–57)
Ginan. or Ginan. adr. (see Ginanni, 1755–57)
Gmelin act. petrop. vol. 3, p. 246 (see Gmelin, 1729)
Gnalt. test. (see Gualtieri, 1742)
Grev. mus. or Grew. mus. (see Grew, 1681)
Gron. lap. (see Gronovius, 1740)
Gualt. test. (see Gualtieri, 1742)
Hasselq. or Hasselqv. itin. (see Hasselquist, 1757)
Hasselqv. act. ups. 1750. p. 33. (see Hasselquist, 1750)
Heyde Ant. Anatome mytulorum 1683 oct (see Heide, 1683)
Imperat. nat. (see Imperato, 1599)
It. gotl. (see Linnaeus, 1747)
It. oel. or oeland (see Linnaeus, 1745)
It. wgot. or wgoth. or wogth. (see Linnaeus, 1747)
Johnst. aquat. or exsangu. (see Jonstonus, 1650–53)
Jonst. aquat. (see Jonstonus, 1650–53)
Kaehl. or Kaehler act. Stockhb. 1754. p.144, t.3, f.A–E or A–F (see Kähler, 1754)
Kirch. mus. (see Buonanni, 1709)
Klein or Klen. ostr. (see Klein, 1753)
Kratz. or Kratzenst. Regenf. (see Regenfuss, 1758)
Labat. itin. (see Labat, 1722)
Lederm. micr. (see Ledermueller, 1760–61)
Lewenh. arcan. (see Leeuwenhoek, 1695)
List. angl. (see Lister, 1678)
List. angl. app. [appendices] (see Lister, 1685, under Lister, 1678)
List. conch. or hist. (see Lister, 1685–92[–97])
List. exer. 2 or exerc. 2 or exereit. 2 (see Lister, 1695)
List. exercit. anat. 1 (see Lister, 1694)
List. exercit. anat. 2 (see Lister, 1695)
M.L.U. or Mus. L. U. (see Linnaeus, 1764)
Mus. Ad. Fr. (see Linnaeus, 1754)
Mus. Tess. or Tessin (see Linnaeus, 1753)
Needham microsc. (see Needham, 1745)
Olear. mus. (see Olearius, 1674)
Osb. iter. or Osbeck. iter. (see Osbeck, 1757)
Pet. or Petiv. amb. or amboin. (see Petiver, 1713)
Pet. or Petiv. gaz. (see Petiver, 1764)
Pet. mus. (see Petiver, 1695)
Planc. conch. (see Plancus, 1739)
Reaum. act. paris. 1712, p. 163 (see Réaumur, 1712)
Regenf. conch. (see Regenfuss, 1758)
Roes. ins. or insect. (see Roesel von Rosenhof, 1746–61)
Rond. aqu. or aquat. (see Rondeletius, 1554–55)
Rond. or Rondel. pise. or test. (see Rondeletius, 1554–55)

Rumph. mus. (see Rumpf, 1705, 1711, 1741)

Scheuch. Diluv. (see Scheuchzer, J. J., 1716)

Scheuch. helv. (see Scheuchzer, J., 1708)

Seb. or Seba mus. (see Seba, 1734–65)

Sellii historia Teredinis. Traject. or Sellii monogr. ultra or Sellii Tered. (see Sellius, 1733)

Sloan. jam. (see Sloane, 1696)

Stobaei Diss. epist. Lund. (see Stobaeus, 1732)

Ström. söndm. 173 (see Ström, 1762)

Swamm. or Swammerd. bibl. (see Swammerdam, 1737–38)

Tessin. epist. 1, n. 28 (not found; apparently a letter to Linnaeus)

Tournef. iter. (see Tournefort, 1717)

Tulp. obs. (see Tulpius, 1739)

Vallisn. nat. (see Vallisnieri, 1721)

Wolff. hass. (see Wolfart, 1719)

Worm. mus. (see Worm, 1655)

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Frederick Benjamin Isely: Biographical Sketch and Malacological Contributions

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Frederick B. Isely was known primarily for his pioneering research in orthopteran ecology (mainly Acrididae and Tettigoniidae) and as an educator/administrator. However, he contributed significantly to the basic knowledge of unionacean biology and ecology. Isely began his studies with freshwater mussels in the Chikaskia River of north-central Oklahoma during 1906. These initial observations soon expanded to include aspects of unionacean ecology, growth, migration, and distributional survey of mussels within the Arkansas and Red river basins of eastern Oklahoma. In these endeavors, he was financially aided through an appointment as a scientific assistant with the U.S. Bureau of Fisheries during the summers of 1910–13. As a result, five manuscripts were published between 1911 and 1931. Isely's innovative concepts for ecological investigations are reflected by his discussion in the 1914 growth paper of the use and value of replicate samples and of the problems encountered using mark/recapture techniques. One such problem was predation by small boys interested in collecting the brass tags used to mark the mussels. The distributional survey, although funded by and conducted for the U.S. Bureau of Fisheries, was delayed in publication due to government reassessment of funding priorities—World War I. This manuscript was published independently by Isely after the war. His last malacological publication resulted from the recovery of one of the "lost" growth study specimens 15 years following the completion of that investigation. Further evidence for the value of replication in research.

Frederick was born June 20, 1873 of Swiss parents (Christian Isely and Elise Dubach) at Spring Grove farm near Fairview, Brown County, Kansas. His early education was gained locally, culminating with his graduation in 1894 from Hiawatha Academy (Hiawatha, Kansas). He entered Fairmount College (now Wichita State University) in its founding year 1895. He was quite active in college activities (*e.g.*, debate team, class president 1895–99) and sports (*e.g.*, track, football) and was awarded a B.S. in 1899, the first 4-year graduating class of the college. In 1909, he earned an M.S. from the University of Chicago and continued that summer with further study at the Marine Biological Laboratory. Later academic

endeavors were pursued during the summers of 1929 and 1931 at the University of Chicago and University of Colorado, respectively.

His teaching career began with an appointment at Franklin Rural School, Brown County, Kansas (1894–95). Following his graduation from Fairmount College,

Figure 1. Frederick B. Isely during his Trinity University years. Reproduced from a photograph given to the Department of Biology, Trinity University by Mrs. F. B. Isely (courtesy of H. D. Murray).

he assumed the principalship of Central School, Hiawatha (1899–1901) followed by stints as teacher of biology at Wichita High School (1901–06) and University Preparatory School, Tonkawa, Oklahoma (1906–12). Equipped with his M.S., he served as professor of biology at Central College, Fayette, Missouri (1912–20) with sojourns during the summers of 1915–17 as instructor of biology at the University of Missouri. His administrative career was initiated with an appointment as dean and professor of biology at Culver-Stockton College, Canton, Missouri (1920–22) followed by his assumption of the same roles at Texas Women's College, Fort Worth (1922–31). He returned to a strictly teaching position as professor of biology at Trinity University, Waxahachie and later San Antonio, Texas (1931–47) where he developed the majority of his orthopteran research. He also served as department chairman from 1931 to 1946, retiring from active teaching in 1946. In recognition of his achievements, Trinity University awarded him the Sc.D. *honoris causa* upon his retirement.

Isely married Mary E. Nickerson of Clearwater, Kansas, on May 8, 1901. They had four children and he appears to have influenced his family, as he did his students; biologists continue in the family to date. In spite of a heavy teaching load, administrative duties, and research, he was active in community organizations throughout his life and still managed time for personal pleasures (*e.g.*, camping, gardening, keeping up with the latest episodes of Joe Palooka and Little Orphan Annie). Isely was a well-loved and enthusiastic instructor in addition to being an active and respected scientist. He received grants-in-aid for his orthopteran research from the National Research Council (1935, 1936) and the American Philosophical Society (1937, 1941). He was a fellow and founding member of the Oklahoma Academy of Science (secretary 1901–12) and the North Texas Biological Society (president 1924–27); a fellow of AAAS and the Texas Academy of Science (president 1938); and a member of the Society of American Zoologists, Ecological Society of America, Entomological Society of America, Kansas Academy of Science, Texas Entomological Society, and Texas State Teachers Association. Frederick B. Isely died December 30, 1947 still active in research. Additional information may be acquired from two memoria (Alexander, 1949; Geiser, 1949).

Recently, a remnant of Isely's malacological collection was rediscovered at the Stovall Museum, University of Oklahoma (Shepard, 1982). About 450 specimens of unionids, representing 37 species remain. Some inade-

quately labeled lots may also be referable to Isely. Thirty-nine specimens including seven species represent vouchers for the 1914 growth paper. Fourteen detached brass tags are also present. The remainder of his collection is from the 1925 distribution survey. Little else of Isely's malacological material, other than some papers in the archives of the Biology Department at Trinity University (H. D. Murray, personal communication), remain.

A small malacological collection of his brother, Dwight Isely, was rediscovered at Wichita State University (Metcalf and Distler, 1984). Further information pertaining to D. Isely may be obtained in Miner (1976) and Metcalf and Distler (1984).

I thank the following people for their kind assistance in providing data for this note: Mrs. Katherine Isely McGuire and Drs. Douglas G. Alexander, Harley P. Brown, Donald A. Distler, Duane Isely, Charles G. Lincoln (deceased), Harold D. Murray, Robert W. Pennak, William D. Shepard, and Gary D. Snell.

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Rediscovery of *Planorbella magnifica* (Pilsbry) in Southeastern North Carolina

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Early in this century, *Planorbis magnificus* was described by Pilsbry (1903) from the lower Cape Fear River region of North Carolina. The type locality for the species was given simply as "lower Cape Fear River". Bartsch (1908) correctly surmised that the species is an inhabitant of lentic environments and found it living in Greenfield Lake, a manmade impoundment lying to the south of what were then the city limits of Wilmington, NC, as well as in Orton Pond, then called Sprunt's Pond, approximately 16 km south of Wilmington. Baker (1945) figured and studied portions of the anatomy of specimens collected by Bartsch and concluded that *P. magnificus* should be reassigned to *Planorbella*. This taxon represents the largest known planorbid.

Planorbella magnifica has not been reported since the accounts by Pilsbry and Bartsch and has been considered extinct by some (Opler, 1976; Imlay, 1977; Palmer, 1985). Fuller (1977) hypothesized that the species may still survive in Orton Pond, a manmade pond similar to Greenfield Lake in age and physiography, based on an observation of large planorbid egg masses there by J. P. E. Morrison.

The Greenfield Lake watershed has been almost totally developed since *Planorbella magnifica* was described, and now undergoes intensive management for control of nuisance algae. Management measures include application of algicides during the growing season and occasional drawdown during winter months. Fuller (1977) mentioned fruitless attempts by himself and others to find *Planorbella magnifica* in Greenfield Lake. Our investigations of that lake indicate that it no longer provides a suitable habitat for this species.

During July 1986, *Planorbella magnifica* was serendipitously rediscovered in Orton Pond, Brunswick County, NC, while collecting water samples. Three living specimens were obtained in 20 minutes. Four empty shells were also collected from the drift line on the shore. During another water-sampling trip in January 1987, an attempt was made to collect live specimens for captive propagation. This effort was unsuccessful as much of the aquatic vegetation had died back. However, two more empty shells were found washed up on the shore.

Our samples of *Planorbella magnifica* vary considerably in size. The maximum shell diameters of the specimens collected alive are 35.5, 21.5, and 16.3 mm. Voucher specimens from our collection have been deposited in the collections of the North Carolina State Museum of Natural History (NCSM P468–P471) and the National Museum of Natural History (USNM 857935). Because of restricted access, additional trips to Orton Pond have not been made.

Live specimens of *Planorbella magnifica* were found on the stems and undersides of the floating leaves of Spatterdock, *Nuphar luteum* (Sibthorp & Smith, 1809), and Fragrant Waterlily, *Nymphaea odorata* (Aiton, 1789). Water depth where living specimens were collected was approximately 1 meter, and the bottom substrate was organic. Orton Pond closely matches Bartsch's (1908) description of habitat suitable to *P. magnifica* in Greenfield Lake.

Like Greenfield Lake, Orton Pond is a manmade impoundment. Both were created early in the last century to serve as a fresh-water source for rice agriculture. Orton Pond exemplifies a type of lentic waterbody unique in southeastern North Carolina. Although blackwater lakes and ponds in the region typically are acidic, Orton Pond's waters have a circumneutral pH, ranging from 6.2 through 7.9 (Smock and Lenat, 1978). We suspect that Orton Pond may have a direct connection to waters of the Castle Hayne aquifer, an Eocene limestone deposit. The molluscan fauna of Lake Waccammaw (Columbus County, NC), the only other sizable circumneutral-pH waterbody in the region, has been investigated frequently (Fuller *et al.*, 1976; Porter, 1985), but *Planorbella magnifica* has not been found in that system. Lake Waccamaw differs from Orton Pond in being much larger, a natural waterbody, and is not a blackwater system.

The owners of Orton Pond undertake little management of the pond and manage the lands that surround it for timber and wildlife. With a continuation of this type of management, the near future for *Planorbella magnifica* seems secure. However, not all of the pond's watershed is protected in this way. Therefore, potentially adverse developments could occur quite some distance from the pond.

Because of the apparent uniqueness of the waters of

Figure 1. Shells of *Planorbella magnifica* collected alive from Orton Pond, Brunswick County, North Carolina, July 1986 (approximately natural size).

Orton Pond and absence of *Planorbella magnifica* in Greenfield Lake and Lake Waccamaw, it appears that the species is extremely restricted in distribution and can be found today only in Orton Pond. We believe that any changes in the quality of the surface waters in Orton Pond's drainage basin or in its underlying groundwater regime may have a deleterious effect on *P. magnifica*. Due to the uncertainty of the future of the pond, an in-depth study of the autecology of the species is needed so that potential conservation measures can be developed and implemented should they prove necessary.

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Bite by *Octopus joubini*: A Case Report

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While octopuses are capable of delivering toxic bites, human case reports are scarce (Halstead, 1978). This report describes a bite by Joubin's octopus (*Octopus joubini* Robson, 1929) in a 12-year-old boy. The incident occurred on Sanibel Island, Florida, on January 2, 1987 at about 0900. A storm had deposited a variety of marine animals on shore from the Gulf of Mexico. Not realizing that octopuses are venomous, the boy, Patrick Reed McKinstry, picked up a small specimen and was promptly bitten on the dorsal surface of the right thumb proximal to the interphalangeal joint. He pulled the octopus away from his thumb within 10 seconds. The actual bite, described as a "sharp pinch", was quickly followed by a burning sensation of greater intensity than a bee-sting. A tiny red spot surrounded by a white circular area 6 mm in diameter was then noticed. Bleeding was minimal, a few small drops. Over the next several hours the thumb became moderately swollen and felt sore, stiff, and, at times, somewhat numb. These symptoms, to a lesser degree, extended to the wrist. Medical attention was not sought because only local effects, which gradually diminished by day one, were noticed. By day three, the thumb was slightly swollen, reddened, and sore, and a tiny hole was noticed at the site. Over the next several days, the thumb became itchy and was treated with 3% hydrogen peroxide solution. This was the first treatment of the bite. By day eight, the swelling and redness had disappeared but some soreness in the metacarpophalangeal joint was experienced. The hole had enlarged to 2 mm in diameter and displayed a slightly irregular border. During the period up to day 12, the hole became darker and a red circular area of up to 7 mm in diameter developed around it. Itching continued but soreness in the joint area decreased. On day 12, a small amount of clear yellow fluid oozed from the hole. The area was then treated with hydrogen peroxide solution and antibiotic ointment. The signs and symptoms gradually diminished, and by day 32 the hole was replaced by a slightly indented circular scar 1 mm in diameter, surrounded by a slightly darkened firm area 6 mm in diameter. By day 100, only the indented scar was evident and the wound was considered completely healed. A shiny, hard circular scar, 1 mm in diameter, was still evident by 1 year. While in excellent health, Patrick is allergic to hymenopteran venoms and to penicillin. However, this was his first exposure to octopus venom, thus, an allergic reaction to explain the bite effects was discounted. Secondary bacterial infection could have contributed to the effects experienced, however, signs of infection, *e.g.*, pus, lymphangitis, and fever, were not observed.

The octopus died after about 2 hours in a pail of sea water and was preserved in 70% isopropyl alcohol. It was identified as a nearly reproductively mature male specimen of *O. joubini* by Dr. Ronald Toll. This species, the smallest of the western Atlantic octopuses, ranges from southern Florida to the Bahamas and the West Indies. Specimens are often washed ashore by storms on the Gulf coast of Florida (Meinkoth, 1981). The dorsal surface of the specimen is deep tan, while the arms and ventral surface are light tan. The mantle is 3.2 cm in length. I have donated this specimen to Dr. Toll's collection.

Two accounts of envenomation following the bite of *O. joubini* were found. In the first (Anonymous, 1965), a physician was bitten on the finger while handling a specimen washed ashore on Sanibel Island, Florida. He experienced a "sharp" bite with a little bleeding, quickly followed by "the most excruciating pain which rapidly became almost intolerable." Within a few hours, the finger became very swollen, hard, and deep red. By the next day, the inflammation and pain had extended to the hand. Later, some white discharge was noted from the bite wound. The swelling and hardness gradually subsided over a period of 2 months. The only systemic effect was a mildly elevated temperature. He noted that "there was never any evidence of bacterial invasion or infection, only an extreme degree of cellulitis."

The second case (Wittich, 1968), occurred on a research vessel off Egmont Key, Florida. A Florida Board of Conservation worker was bitten on the back of the hand while sorting marine specimens. In this case, "a sharp, piercing sensation" was felt, and a "severe pain" extended to the upper arm. The bite wound bled slightly and almost instantly became surrounded by a "pure white

welt of about 25 mm diameter." In the following hour, the victim experienced pain and swelling around the bite, accompanied by nausea, headache, and fever. Improvement gradually occurred, but after 3 days the area was still sensitive and swollen. The swelling persisted, and some itching and a serous discharge from the wound occurred. After 1 month, a 2 mm wound surrounded by a 6 mm red periphery was present. The wound then healed quickly.

In the case I report, the bite effects were not as severe as those noted above even though the victim was a child with less tissue mass to dilute the venom. However, the amount of venom delivered could have been minimal.

ACKNOWLEDGEMENTS

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Occurrence of Mites in Mexican Land Snails

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To date there has only been a single report (Baker, 1945) of mites infecting the mantle cavity of a land snail from Mexico (*Helix pomatia* Linné, 1758, an introduced species). The mite was identified as *Riccardoella oudemansi* (Thor, 1932), however, the mite shown by Baker (1945) is similar to the figure published by Fain and Van Goethem (1986) for *Riccardoella limacum* (Schrank, 1776) (Prostigmata: Ereynetidae). This mite has been studied by several European authors (Turk & Phillips, 1946; Baker, 1970) and reported as cosmopolitan.

In this note, we report findings of mites parasitizing the mantle cavities of two species of land snails of the family Bulimulidae and one species referable to the family Helicidae. The bulimulid *Bulimulus unicolor* (Sowerby, 1833), collected in Tomas Garrido, in the state of Quintana Roo, was parasitized by *Riccardoella limacum*, with one protonymph and one deutonymph collected from nearly 50 specimens of the snail. Of 79 specimens of *Rhabdotus alternatus* (Say, 1830), another bulimulid collected in Xicotencatl in the state of Tamaulipas, that were examined, one contained three mites of the genus *Boydaia* (Ereynetidae) and another contained a single specimen of *Eupodes voxencollinus* (Sig Thor, 1934). This is the first report of the last two mite species on land snails.

Examination of other land snail species of the families Helicidae, Achatinidae, Succinidae, Oleanicidae, and Polygyridae revealed no evidence of parasitism by mites, with the exception of a single specimen of *Helix aspersa* (Müller, 1774), an introduced species collected in Mexico City, which was infected with two specimens of *E. voxencollinus*. As no mites were found in any Mexican land snails from the above families, the family Bulimulidae remains the only new record of a host for mites.

The examined snails are deposited in the Mollusk Collection of the Departamento de Prehistoria, I.N.A.H., and the mites in the Acarology Collection of the Laboratorio de Acarologia of the E.N.C.B.

We acknowledge two anonymous reviewers for their critical comments to improve this paper.

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Axelella, New Name for *Olssonella* Petit, 1970, a Preoccupied Taxon (Mollusca: Cancellariacea)

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The cancellariid genus *Olssonella* Petit, 1970, was proposed for a rather compact and well-defined group of species from the Later Tertiary and Recent faunas of the Americas. An Eastern Atlantic species was subsequently placed in this genus by Bouchet and Warén (1985:263), and the morphology of the type species was published by Harasewych and Petit (1984). The taxon has been used by a number of other authors since it was proposed. Unfortunately, it has just been noted that *Olssonella* is preoccupied, and a replacement name is here proposed.

Axelella, new name for *Olssonella* Petit, 1970:83.
Not *Olssonella* Glibert & Van de Poel, 1967:121.

Type species, by original designation of *Olssonella* Petit, 1970, *Cancellaria smithii* Dall, 1888, Recent, Western Atlantic.

This new name honors the late Axel A. Olsson, as did the name it replaces, and the name which makes the replacement necessary.

Appreciation is expressed to Dr. Philippe Bouchet, Muséum National d'Histoire Naturelle, Paris, for calling the prior use of *Olssonella* to my attention.

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CONTENTS

A New Species of *Alvania* (Rissoidae) from the West Indian Region

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ABSTRACT

Alvania (Alvania) colombiana new species was found from 45 to 261 m (24 to 143 fms) depths off the Caribbean coast of Colombia to South Florida, the Gulf of Mexico, and Puerto Rico. *Alvania colombiana* differs from *Rissoa xanthias* (Watson, 1886), in having a protoconch with a single spiral zig-zag line of tiny nodules just above the suture, and by its smaller shell size. *Alvania colombiana* also differs from *Rissoa precipitata* (Dall, 1889), by its protoconch and size.

INTRODUCTION

Exploration of the deep sea a century ago was the equivalent of the space age today. The famous "Challenger" expedition sampled two offshore stations in the tropical western Atlantic in which small mollusks were numerous. These were described by Watson (1886). Among the Rissoidae were two species, *Rissoa pyrrhias* (Watson, 1886) and *Rissoa xanthias* (Watson, 1886), that were similar in size and shape. Dall (1889), reporting on the "Blake" material, described two more species of *Rissoa*, *Rissoa acuticostata* and *Rissoa precipitata*. *Rissoa acuticostata* was similar to *Rissoa xanthias*, and finally Dall (1927) acknowledged that with more specimens it was impossible to separate the material into two species. *Rissoa precipitata*, on the other hand, is known principally from the original description and illustration.

There is another small western Atlantic rissoid which at first glance appears similar to the illustration of *Rissoa precipitata*. However, there are a number of features that differentiate them. Size is one: the small species has an average adult size of 1.2 mm while *Rissoa precipitata* (holotype) has an adult size of 3.92 mm. Protoconch is the other: the small species has a projecting protoconch while *Rissoa precipitata* has a depressed protoconch. One of us (D.R.M.) had obtained specimens of the small species during the MAFLA (Mississippi, Alabama, and Florida) study (1974 to 1975) in the eastern Gulf of Mexico. This small species was first reported by one of us (N.S.R.) as *Alvania* sp. 1 (see literature cited; Rodriguez, 1983).

ABBREVIATIONS

USNM = National Museum of Natural History, Smithsonian Institution.
FSBS 1 = Florida Department of Natural Resources, Marine Research Laboratory, St Petersburg.
MCZ = Museum of Comparative Zoology, Harvard University.
UMML = University of Miami Marine Laboratory.
CNMS = Colombian Natural Museum of Science, National University, Bogotá

MATERIALS AND METHODS

All the specimens to be photographed in the SEM were cleaned in 100% sodium hypochlorite for 2 minutes, then rinsed in distilled water twice. If the specimens still showed residual material (*e.g.*, sand grains), they were sonicated for 60 seconds. Finally, the specimens were air dried and put on a SEM stub with double-sided Scotch tape.

Alvania (Alvania) colombiana new species
(figures 1, 2)

Description: Shell 1.0 to 1.3 mm in length. Protoconch multispiral, glossy, light brown, with 3½ whorls that are sculptured with 1 spiral zig-zag line of tiny nodules just above the suture and 1 undulating line of the same nodules in the middle of the whorl. Nodules irregularly arranged over entire protoconch. Teleoconch of approximately 2 whorls, with numerous axial ribs. Adult shell translucent, very light brown in color.

Axial ribs slightly curved, 26 ribs on the body whorl fading out on the base of the shell. Body whorl with a narrow spiral groove just below the suture and another 7 to 9 grooves between the periphery of the final whorl and the base of the shell. Varix terminal with a narrow extension forming outer lip of semilunate aperture. Some specimens weakly umbilicate.
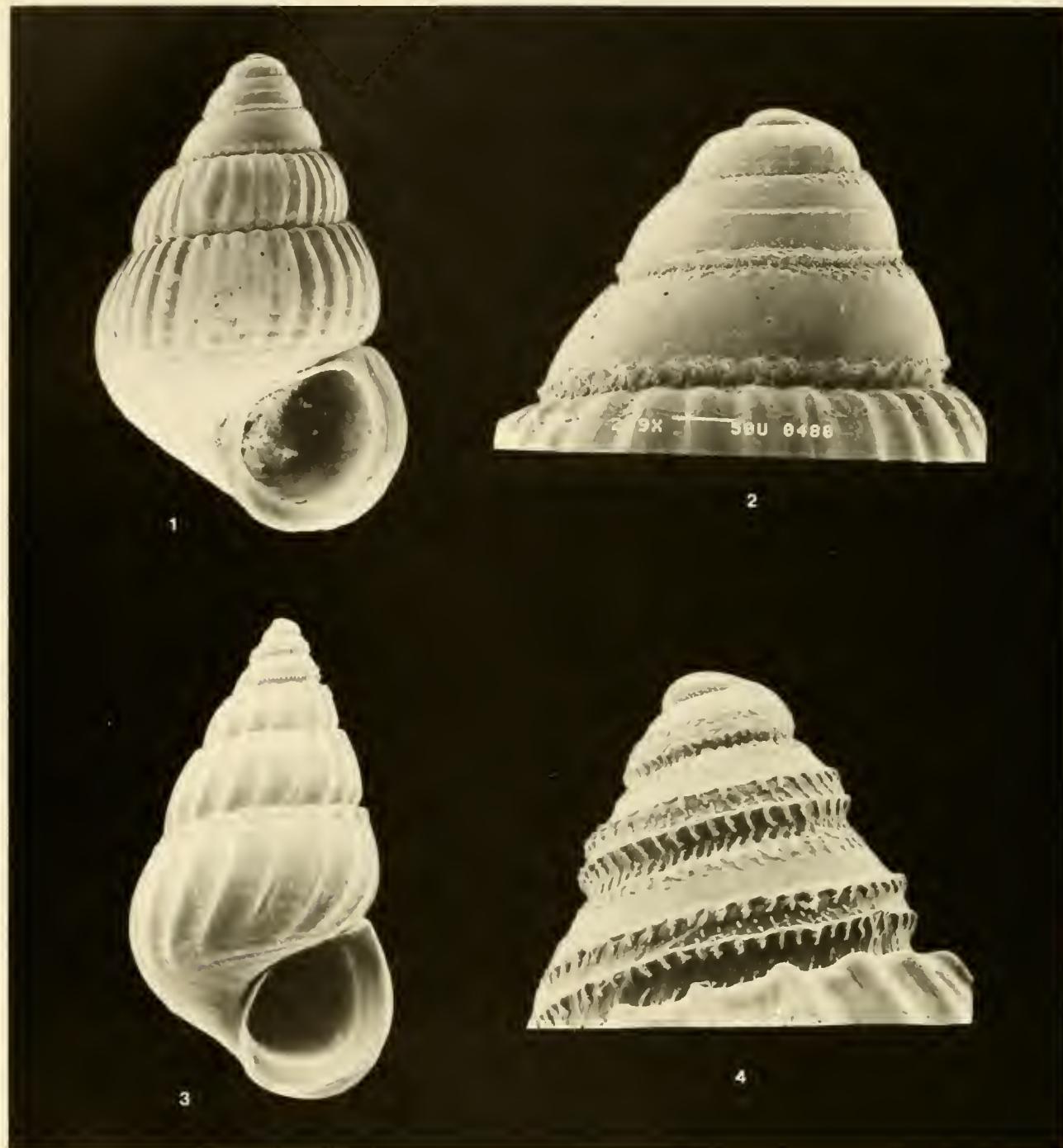
Figures 1, 2. *Alvania colombiana* new species. **1.** Holotype, USNM number 859339, 1.28 mm in length. **2.** Protoconch, 280 ×. **Figures 3, 4.** *Rissoa xanthias* (Watson, 1886), from off Miami, in the junior author's collection, 2.26 mm in length. **4.** Protoconch, 220 ×.

Type locality: Off the west coast of Florida at 29°35′N, 87°20′06″W, depth 107.3 m.

Holotype: USNM number 859339. Length, 1.28 mm. Width, 0.78 mm.

Paratypes: One from off the west coast of Florida at 29°35′N, 87°20′06″W, depth 107.3 m, USNM number

859340; 2 from off the west coast of Florida at 28°24′N, 85°15′06″W, depth 164.6 m, FSBC I number 33113; and off the west coast of Florida at 29°49′30″N, 86°25′30″W, depth 82.3 m, FSBC I number 33114; 2 from off Puerto Rico at 17°53′24″N, 66°35′10″W, depth 221 m, MCZ number 297220; and off Miami at 25°47′N, 80°01′30″W, depth 137 m, MCZ number 297219; 2 from off Miami
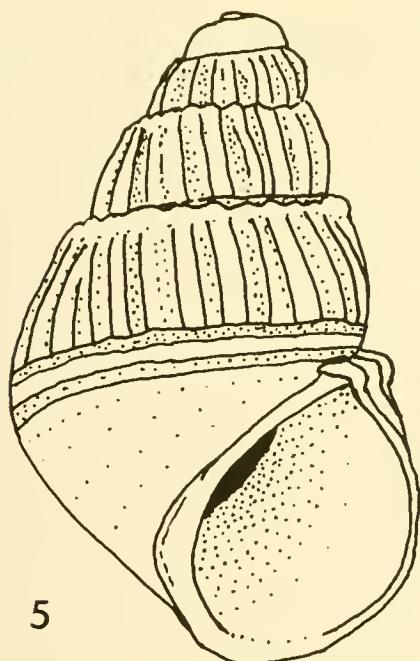
Figure 5. Drawing of *Alvania precipitata* (Dall, 1889), holotype, MCZ 7470, 3.92 mm in length.

at 25°47'N, 80°01'30"W, depth 137 m, UMML number 8349; and off Miami at 25°46'30"N, 80°00'08"W, depth 76.81 m, UMML number 8350; 2 from off the Caribbean coast of Colombia at 09°52'35"N, 75°47'25"W, depth 72 m, CNMS number ICN-MHN(MO)522; and off Miami at 25°46'30"N, 80°00'08"W, depth 76.81 m, CNMS number ICN-MHN(MO)523.

Distribution: This species was found in 31 samples from off the Caribbean coast of Colombia collected between 1979 and 1981. The specimens were found at depths ranging from 45 m to 261 m, but were most abundant at depths between 65 m and 160 m. Other specimens of this species were found from off the west coast of Florida, off southern Puerto Rico, and the Straits of Florida east of Miami. The bottom in almost all cases consisted of sandy mud. The species is probably found in these depths throughout the Caribbean, the southern and eastern Gulf of Mexico, and the Bahamas. All the specimens were found dead.

Discussion: *Alvania colombiana* appears to be a common widespread species throughout the Caribbean and adjacent areas. This is a very small compact species that should not be confused with any other in its range. Some features, however, are lacking or lost on the protoconch of some specimens. These include the fine nodules distributed all over the protoconch, and the undulating line of nodules on the periphery. These features are seen only under high magnification, so are difficult to observe for routine identification. Details of the teleoconch sculpture, however, should be easy to make out under low power, even in a somewhat worn specimen.

Alvania colombiana has been confused with *Rissoa precipitata* (Dall, 1889) (figure 5). This was due to the fact that specimens of *Rissoa precipitata* were not available for comparison. The holotype and only known specimen, MCZ 7470, is a thin shell with no terminal varix. In fact, the sculpture fades away almost completely on the last half whorl (except for the sub-sutural tubercles). The protoconch is of the form seen in gastropods without a planktonic larval stage: large, rounded, unsculptured, and with a smooth transition from protoconch to teleoconch. The type locality is Yucatan Strait at a depth of 640 fathoms (not 670 as is given by Dall, 1889:280).

Another similar species is *Rissoa xanthias* (Watson, 1886) (figures 3 and 4). It, however, is about twice the size, has just over half as many axial ribs, and has a different and very distinctive protoconch. In this species the protoconch has 3½ whorls, in which the sutures are deep and ornamented with a line of spirally arranged vertical pustules. Just above the suture there is a wide canal whose edges are formed by an undulating line with vertical pustules equally spaced and directed downward. Each canal also has in the middle dots and small nodules randomly distributed. Watson reported it from Challenger Sta. 24 off Culebra Island, 18°38'30"N, 65°05'30"W, depth 715 m, and from Sta. 122, 9°10'S, 34°49'W to 34°53'W, depth 640 m.

Finally, *Rissoa pyrrhias* (Watson, 1886) is another similar species. It is slightly larger than *Rissoa xanthias*, and its spiral grooves are not confined to the base of the shell. According to Watson (1886), the protoconch has 2½ whorls which are scored with coarse but feeble spiral threads.

ACKNOWLEDGEMENTS

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Micromorphology of Neogastropod Egg Capsules

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ABSTRACT

Egg capsule micromorphology of eight species of neogastropods (*Chicoreus florifer dilectus, Phyllonotus pomum, Cantharus multangulus, C. cancellarius, Conus floridanus floridensis, C. jaspideus stearnsi, Granulina ovuliformis,* and *Marginella aureocincta*) was studied with light microscopy by examining very thick, toluidine blue stained sections. Laminae exposed by fracturing the sections, and their reactions to the stain, provided the characters used to describe micromorphology.

The results showed that muricaceans and buccinaceans have complex but microstructurally similar egg capsules, while conids and marginellids have egg capsules with taxonomically distinct microstructural characteristics. In the Muricacea and Buccinacea, four structural laminae of similar origin and function are usually present in the capsule wall, the second from the outermost having the most complex pattern of fibers and the greatest thickness. The third outermost lamina is continuous with one or more components sealing the escape aperture. In some buccinaceans, only a trace of the third lamina exists in the wall. Four layers, including one or two mucoid plugs, close the escape aperture. Conid egg capsules differ in that they include only three structural laminae in the capsule wall and three layers, including a mucoid plug, sealing the escape aperture. Microstructure and fiber pattern in the middle lamina are probably unique to this family. Egg capsules of marginellids have a distinctive thin, dense wall not separated into laminae and lack an escape aperture closed by a mucoid plug. There is a preformed suture that fractures at hatching in the wall of most marginellid egg capsules.

Key words: Reproduction; egg capsules; Neogastropoda; *Chicoreus; Phyllonotus; Cantharus; Conus; Granulina; Marginella.*

INTRODUCTION

Encapsulation of early ontogenetic stages is typical of higher gastropods, especially neogastropods. The highly refractory, layered envelopes of carbohydrate and protein are structurally and chemically complex (Hunt, 1971; Flower, 1973; Goldsmith *et al.*, 1978; Gruber, 1982; Sullivan and Maugel, 1984). Encapsulation and the formation of egg masses provides protection and has considerable survival value (Tamarin and Carriker, 1967; Pechenik, 1979, 1983; Abe, 1983; Lord, 1986). Although there are thousands of neogastropod species, it still has not been clearly established how the egg capsules are formed in the oviduct and ventral pedal gland. Nor is it known if a common capsular microstructure exists in various neogastropod taxa.

Macromorphology of the often species-specific egg capsules and egg masses produced by neogastropods has been studied more frequently than any other aspect of neogastropod egg encapsulation. This was illustrated in the review of prosobranch reproduction by Webber (1977), in a more recent review of egg encapsulation for all mollusks by Pechenik (1986), and in descriptive reports on the external structure of neogastropod egg capsules by Bandel (1975, 1976a,b,c, 1982) and D'Asaro (1986a).

In early reports on neogastropod capsule-wall micromorphology (*e.g.,* Ankel, 1937; Hancock, 1956), three or four laminae were described, including specific patterns of fibers. However, it was not established if these are structural relationships common to the species studied or to higher taxa. Fretter (1941) provided for *Nucella lapillus* (Linné, 1758), *Ocenebra erinacea* (Linné, 1758), *Nassarius reticulatus* (Linné, 1758), and *Buccinum undatum* Linné, 1758 the most frequently cited descriptions of how these neogastropods construct, in the oviduct and ventral pedal gland, three or four layered capsules.

To characterize the laminated egg capsule of *Urosalpinx cinerea follyensis* B. Baker, 1951, Tamarin and Carriker (1967) published the first comprehensive study employing light microscopy—including polarized light—and electron microscopy. They described a capsule with four laminae composed of asymmetrical protein-like molecules bound into collagen-like matrices. They also noted that the great structural complexity of the capsular wall could only be partially explained by Fretter's (1941) description of the formative process. Bayne (1968) conducted a histochemical study of several gastropod egg capsules, including those of *Nucella lapillus*, and found mucopolysaccharides in at least three capsular laminae of that species. He was one of the first to use toluidine blue for this purpose. Flower *et al.* (1969) and Flower (1973) described the origin and the ultrastructure of neogastropod capsular proteins. In another histochemical study, Gruber (1982) described six structural layers in the capsule wall of *Eupleura caudata etterae* B. B. Baker, 1951, and three additional layers associated with the escape aperture and layers of albumen.

Table 1. Comparative micromorphology of muricacean egg capsules stained in most cases with toluidine blue (meta = metachromatic, mp = mucoid plug, nr = not reported, ortho = orthochromatic, pre = present, tt = two types of albumen cells in the oviduct, z = zone).

Species	Width of wall	L1	L2	L3	L4	Layers closing aperture	Layers of albumen	Author
Chicoreus florifer dilectus	64 μm	meta, 4 μm	meta, 54 μm	meta, 2 μm	meta, 4 μm	L1, mp, L3 (mp), L4, 315 μm	two meta	this report
Phyllonotus pomum	51 μm	meta, 1–2 μm	ortho in part, 47 μm	meta, 1–2 μm	meta, 2 μm	L1, L3 (mp), mp, L4, 429 μm	two? meta	this report
Nucella lapillus	nr	meta	pre	meta	nr	L3? (mp)	meta matrix	Ankel, 1937; Fretter, 1941; Bayne, 1968
Urosalpinx cinerea	109 μm	ortho, 30 μm	ortho, 75 μm	pre, 2 μm	ortho, 2 μm	outer z, dense z, L3 or diffuse z, L4, 500 μm	pre	Hancock, 1956; Tamarin and Carriker, 1967
Ocenebra erinacea	nr	nr	pre, two fibrous layers	pre, mucoid layer	nr	mp	tt	Fretter, 1941
Eupleura caudata etterae	nr	meta, (1)*	(2–5)	(6?–7)	meta (8)	(1, 6?, 7 = mp, 8)	two meta	Gruber, 1982

* Ten layers were described; possible relationships for eight are indicated in parentheses.

In the most comprehensive and detailed study to date, Sullivan and Maugel (1984) used transmission and scanning electron microscopy, histochemistry, and polyacrylamide gel electrophoresis to examine the egg capsule of *Ilyanassa obsoleta* (Say, 1822). They were able to determine the physical and chemical structure of the capsule wall and confirm the origin of four structural laminae in the oviducal capsule gland. A fifth, nonstructural layer was identified as a product of the ventral pedal gland.

Since the previous work did not consider egg capsule micromorphology in a taxonomic perspective, the purpose of this study was to describe the complex laminar structure of egg capsules from two species in each of four diverse neogastropod taxa: Muricacea, Buccinacea, Marginellidae, and Conidae. These descriptions, as well as those in a few papers with similar data, were used to compare neogastropod egg capsule micromorphology in order to determine if there is a common wall structure in the selected taxa, and indirectly, if a common mechanism to produce neogastropod egg capsules exists.

MATERIALS AND METHODS

The eight species from St. Joseph Bay in northwest Florida selected for study are listed in tables 1–3. Egg capsule macromorphology of each species is known (refer to the Results for citations and museum voucher numbers). Specimens for sectioning were preserved in 10% buffered seawater formalin, a fixative considered acceptable be-

cause egg-capsule proteins are very stable in a range of acids and bases and are only slightly soluble when autoclaved in water (Hunt, 1971). Capsules were taken from near the center of well-formed egg masses, or if deposited individually, they were selected to represent the average size and shape for that species.

To determine the number of egg capsules per species that must be sectioned to account for possible variations in staining and micromorphology, preliminary histological procedures were performed on two egg capsules from each of five egg masses of *Cantharus multangulus* (Conrad, 1846) deposited by different females. Although the sectioned capsules were not microstructurally identical, a recognizable pattern of structural laminae existed among all capsules produced by the same and different females of this species. Because the pattern for *C. multangulus* could be recognized in each sectioned capsule and the literature suggested that it existed for other neogastropod species, sections for the remaining seven species were prepared from only two or three egg capsules produced by different females.

After fixation, the larger egg capsules were opened along one edge in the longest axis with a scalpel to accelerate diffusion of the embedding fluids. Following dehydration in ethyl alcohol, capsules were cleared in toluene and embedded in paraffin (melting point = 56 °C).

Capsules were sectioned at 20–22 μm. All sections were parallel to the longest axis and included some that passed through the sealed escape aperture and the basal plate. To separate structural laminae, the capsule wall was frac-
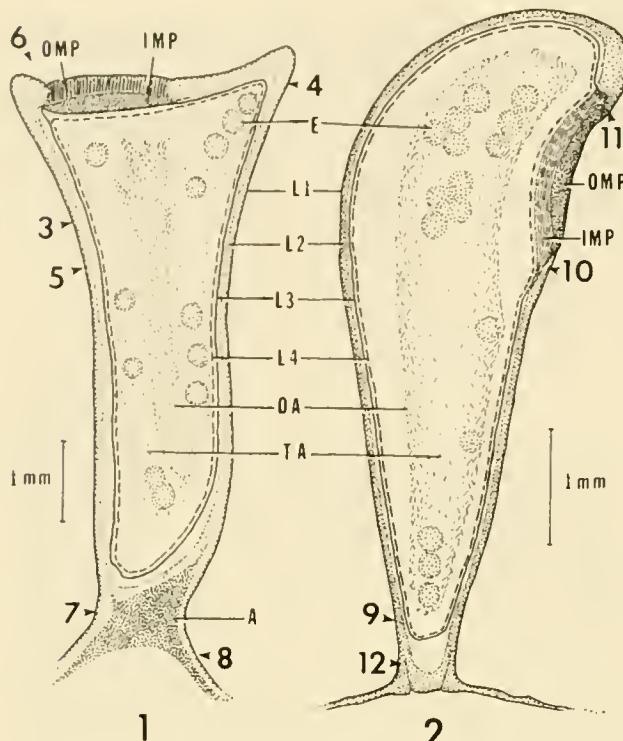
Figure 1. Schematic drawing of a longitudinally sectioned egg capsule of *Chicoreus florifer dilectus*. **Figure 2.** Drawing, like figure 1, of a *Phyllonotus pomum* egg capsule. Numbers with arrowheads indicate positions at which photographs for figures 3–12 were taken. Empty spaces in figures 1 and 2 are artifacts produced during dehydration. A = adhesive, DA = dense albumen, E = embryo, IMP = inner mucoid plug, L1 = metachromatic first lamina—solid line, L2 = second lamina—light stipple, L3 = metachromatic third lamina—solid line, L4 = metachromatic fourth lamina—broken line, OMP = outer mucoid plug, TA = thin albumen. L2 is metachromatic in figure 1 and partially orthochromatic in figure 2.

tured and partially delaminated by varying the speed at which the microtome blade cut a section.

To demonstrate mucopolysaccharides, sections were stained with toluidine blue for 1.5–2.0 minutes according to the method of Gurr (1962:440). They were then rapidly dehydrated in ethyl alcohol, cleared in toluene, and mounted in methyl methacrylate.

Egg capsule microstructure was examined using light microscopy. Observation of the preliminary sections suggested that toluidine blue metachromasia would produce a range in color from purple through heliotrope (reddish purple) but rarely red. Also, some layers would be orthochromatic (blue) or colorless. In the intact capsule wall, structural laminae were difficult to trace by following metachromatic layers alone. However, when a struc-

tural lamina was first isolated and defined in a fractured or delaminated section, then the lamina could be rapidly and comparably traced in whole, stained sections. If a capsule fractured and delaminated repeatedly in a consistent pattern, then the parts were considered distinct structural laminae produced by different types of cells or produced at different times. Those less than a few micrometers wide could be recognized when they separated from the sections and folded to one side. Very thick sections also allowed microsculpture on the outer laminar surface to be examined (*e.g.*, figure 3). Following Tamarin and Carriker's (1967) method, structural laminae were identified from outermost to innermost as L1–L4. Diagrams of median sections were prepared with a drawing tube mounted on a compound microscope, while photomicrography was used to record microstructure at selected positions on a section.

Measurements of the capsule wall, structural laminae, and the sealed escape aperture were taken from the middle regions of each (tables 1–3). These dimensions should be considered approximations, as Sullivan and Maugel (1984) suggested, because of possible shrinkage introduced by the method and the wide range in width occurring at approximately the same position on different capsules of the same species.

RESULTS

Chicoreus florifer dilectus (A. Adams, 1855)
(figures 1, 3–8; table 1; USNM 860426)

Egg capsules of this muricid are distinctly vasiform in section (figure 1). Macromorphology was described by D'Asaro (1970:420, fig. 3).

The capsules have a thick, highly fibrous wall in which four structurally distinct components can be identified: L1, a thin, finely fibered, metachromatic outer lamina; L2, a metachromatic lamina, with layered, coarse fibers forming the bulk of the wall; L3, the thinnest metachromatic lamina, closely applied to the innermost layer; and L4, a metachromatic lamina surrounding the albumen (figures 3, 4; table 1). L1 is so transparent that the coarser L2 fibers can be seen through it. Except on the stalk and basal plate, L1 is folded in a corrugated manner (figures 3, 4, os). L2 may have fibers directed at right angles or parallel to the long capsule axis and arranged with regional differences in two or three fused layers. When three fibrous components are present, the middle one has the coarser fibers arranged parallel to the long axis (figure 3, L2). Where the wall was folded during formation, L2 fibers separate, forming large vacuoles (figure 4, v). These vacuoles are not stained and are probably filled with a nonmucoid liquid. L2 fibers fuse with a more or less homogeneous inner component in

Figures 3–8. Sections of the *Chicoreus florifer dilectus* egg capsule. **3.** Wall showing laminae. **4.** Wall just below the apical plate. **5.** Albumen fibers. **6.** Mucoid plugs in the escape aperture at the junction with L2. **7.** Wall in the stalk. **8.** Basal plate and adhesive. Positions at which photographs were taken are indicated on figure 1. a = adhesive, da = dense albumen, f = fracture, fL3 =
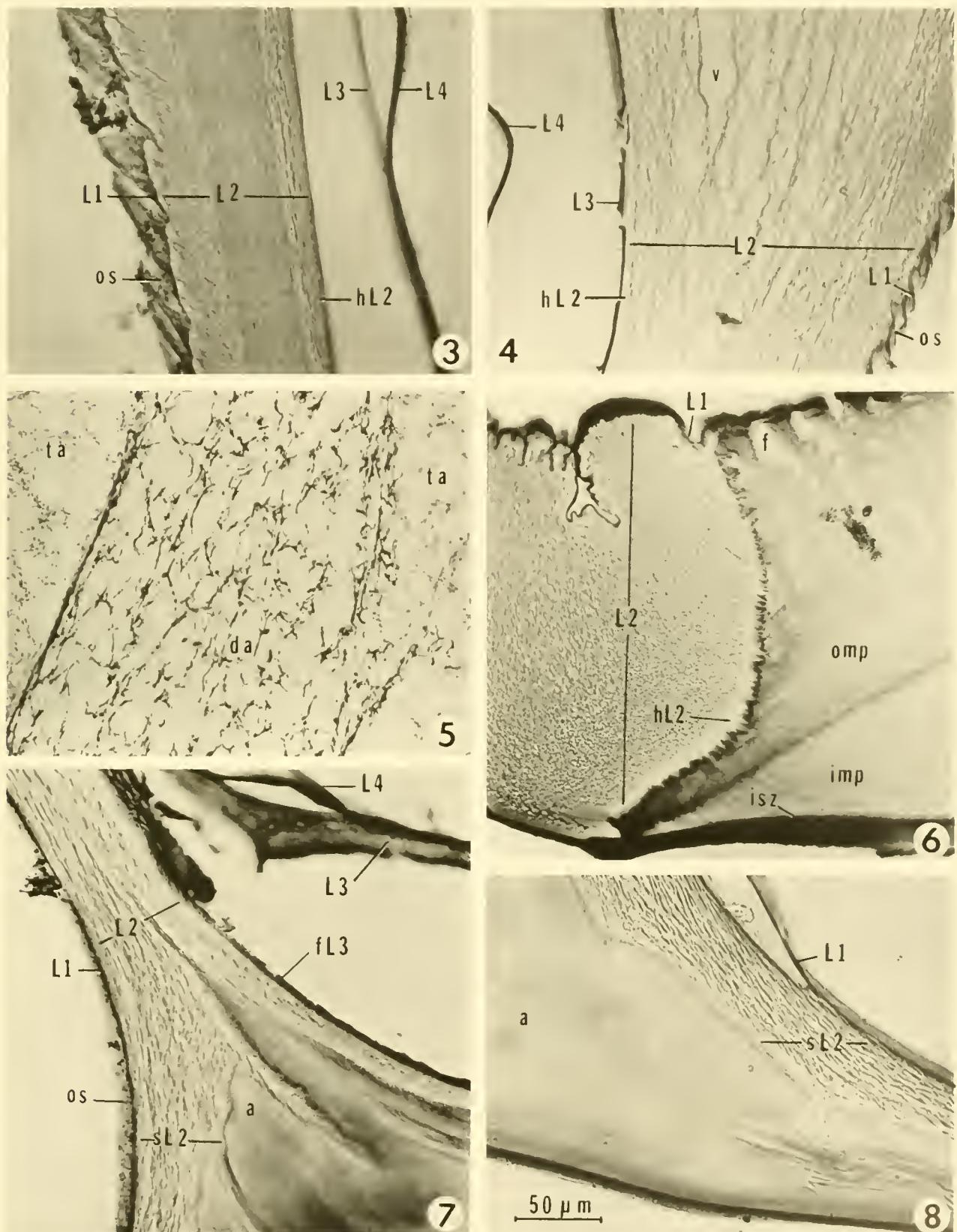
fragment of L3, hL2 = homogeneous component of L2, imp = inner mucoid plug, isz = intensely stained zone, L1 = metachromatic first lamina, L2 = metachromatic second lamina, L3 = metachromatic third lamina, L4 = metachromatic fourth lamina, os = outer surface of L1, omp = outer mucoid plug, sL2 = outer portion of L2 in the stalk, ta = thin albumen.
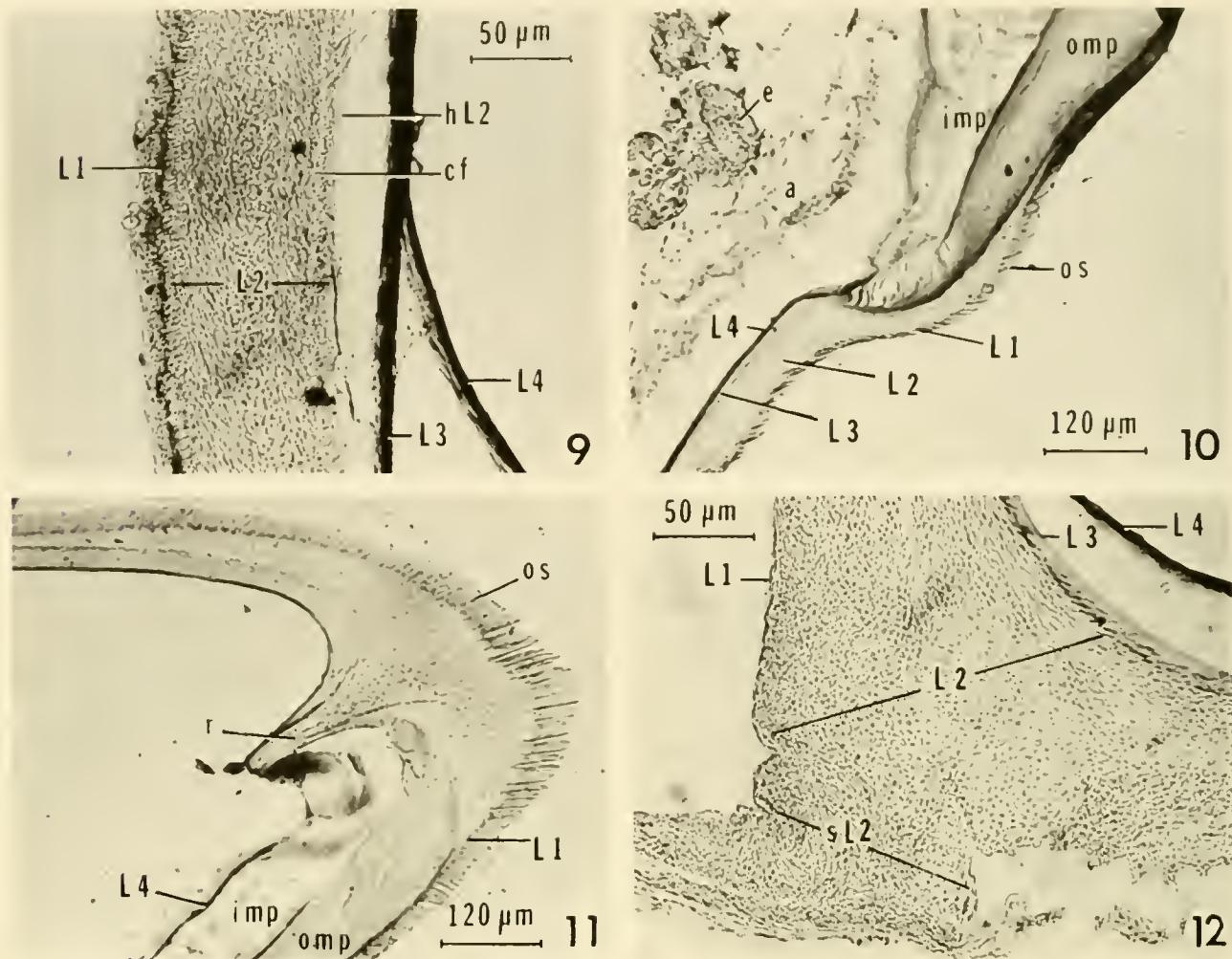
Figures 9–12. Sections of the *Phyllonotus pomum* egg capsule. **9.** Wall showing all laminae. **10.** Escape aperture toward the base. **11.** Escape aperture toward the apex. **12.** Stalk and basal plate. Positions at which photographs were taken are indicated on figure 2. a = albumen, cf = circular fibers, e = embryo, hL2 = homogeneous component of L2, imp = inner mucoid plug, L1 = metachromatic first lamina, L2 = partially orthochromatic second lamina, L3 = metachromatic third lamina, L4 = metachromatic fourth lamina, omp = outer mucoid plug, os = outer surface of L1, sL2 = outer portion of L2 in the stalk, r = ridge.

contact with L3 (figures 3, 4, hL2). L3 stains less intensively than L4. In the apical plate, L3 appears to fuse with the inner mucoid plug and may have similar composition. As described by Ankel (1929: fig. 1) for *Nucella lapillus* and Franc (1940: fig. 2) for *Ocinebrina aciculata* (Lamarck, 1822), L4 completely surrounds the albumen and probably contains it during assembly of the capsule while other components are more fluid. Hereafter, L4 will be called the albumen retaining layer.

Two structurally distinct types of albumen occur: an outer layer including metachromatic fibers with randomly attached granules in which all embryos are situated (figures 1, TA; 5, ta) and, an inner core including denser strongly metachromatic fibers (figures 1, DA; 5, da). Fibers of dense albumen may fuse in a continuous layer where the albuminous components meet; however, the fused layer did not delaminate during sectioning. The thin outer albumen does not envelop the denser core basally (figure 1).

The apical escape aperture is closed by a structurally complex barrier composed of four layers (figures 1, 6). L1 is contiguous with the outer layer. The metachromatic (purple) second layer or outer mucoid plug is larger than the aperture and interdigitates with but is clearly separated from the homogeneous inner component of L2 (figure 6, omp, hL2). Fractures across the width of the outer mucoid plug apparently caused during sectioning occurred (figure 6, f). The third layer is a lenticular, heliotrope mucoid plug, larger than the aperture, which sometimes fractures during sectioning. L3 is fused to the lenticular or inner plug in an intensely stained zone (figure 6, isz). L4 is the innermost layer closing the escape aperture and is fused to L3 in the same intensely stained zone.

The stalk and basal plate are formed from the capsule wall and an adhesive material (figures 1, A; 7, 8, a). The outer portion of both includes L1 and up to the longitudinal, fibrous component of L2 (figure 7, sL2), while

the base of the capsular lumen is formed from the remaining parts of L2 as well as L3 and L4. Mucoid adhesive, which has orthochromatic and metachromatic zones and occasional L2 fibers, fills the center of the stalk (figures 7, 8, a).

Phyllonotus pomum (Gmelin, 1791)
(figures 2, 9–12; table 1; USNM 860425)

The somewhat tongue-shaped capsules and the rather massive, communal egg masses were described by Perry and Schwengel (1955: fig. 338), D'Asaro (1970:422, fig. 3), Radwin and Chamberlin (1973:107, fig. 1), Bandel (1976a:10, fig. 4), and Moore and Sander (1978:253, fig. 2). Unlike *Chicoreus florifer* egg capsules, those of *Phyllonotus pomum* may have two points of attachment with a supporting substratum that nearly always is a conspecific capsule. Sections of such capsules are very variable in outline.

Phyllonotus pomum capsules have a distinctly fibrous wall that is only partially metachromatic (table 1). Four structural parts exist: L1, a thin, metachromatic outer lamina; L2, a thick, coarsely fibered and partially orthochromatic lamina; L3, a strongly metachromatic component; and L4, a metachromatic albumen retaining layer (figures, 2, 9). L1 is as transparent as the homologous lamina in *Chicoreus florifer dilectus* and is corrugated on or near folds in the wall (figures 10, 11, os). L2 remains almost unstained. It has a core of longitudinal fibers bordered in most areas by a few circular fibers (figure 9, L2, cf). Each side of the fibrous zone may be bordered by a narrow, faintly orthochromatic, homogeneous zone (figure 9, hL2). L3 has no obvious fibers and appears fused to the outer mucoid plug of the escape aperture, as noted later. L4 has distinct circular fibers arranged in a single layer.

Albumen, including fibrous and amorphous material, is present in sections only near the retaining layer (figure 10, a). This distribution is an artifact, as noted in *Cantharus cancellarius*, caused by loss of the more fluid contents during dehydration. Embryos are distributed in both components of the albumen.

Positioned on one side of the capsule, the sealed escape aperture includes four layers (figures 10; 11, L1, omp, imp, L4). The outer component is formed from L1. The second outermost layer, including intensely stained metachromatic regions, is continuous with but distinct from the homogeneous proximal part of L2, and appears to be fused or continuous with L3. This pattern is different from that of *Chicoreus florifer dilectus*. A third layer, which is metachromatic, mucoid with small vesicles, and exceedingly fragile, bulges into the capsular lumen, where it is bordered by L4, the albumen retaining layer. The more apical and lateral borders of the escape aperture, formed from L2, have an inward projecting ridge (figure 11, r).

The basal plate is formed from L1 and the outer half of L2. A separation occurs in a dense reticulum or vacuolated zone near the midline of the lamina (figure 12,
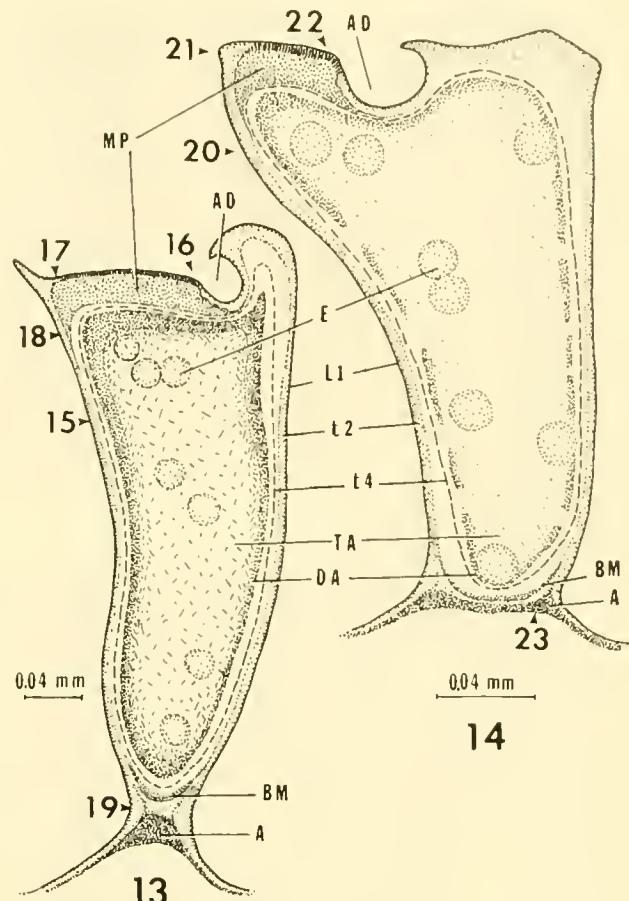

Figure 13. Schematic drawing of a longitudinally sectioned egg capsule of *Cantharus multangulus*. **Figure 14.** Drawing, like figure 13, of a *Cantharus cancellarius* egg capsule. Empty spaces in figures 13 and 14 are artifacts produced during dehydration. Numbers with arrowheads indicate positions at which photographs for figures 15–23 were taken. A = adhesive, AD = apical depression, BM = basal mucoid material, DA = dense albumen, E = embryo, L1 = orthochromatic first lamina—solid line, L2 = second lamina—light stipple, L4 = metachromatic fourth lamina—broken line, MP = mucoid plug. TA = thin albumen.

sL2). Where the outer half of L2 was in contact with the substratum, a homogeneous zone having some fibers extending through it toward the substratum is present. The inner half of L2, L3, and L4 form the floor of the capsular lumen. No adhesive layer was observed on capsules that had been attached to those of conspecifics.

Cantharus multangulus (Philippi, 1848)
(figures 13, 15–19; table 2; USNM 947143)

Macromorphology of the egg capsule was described by Perry and Schwengel (1955: fig. 340), Radwin and Chamberlin (1973:110, fig. 6), and D'Asaro (1986a:85, fig. 3). Median sections through the ribbed and spined capsule are roughly vasiform in outline and have a rounded, apical depression partly covered by a transverse ridge
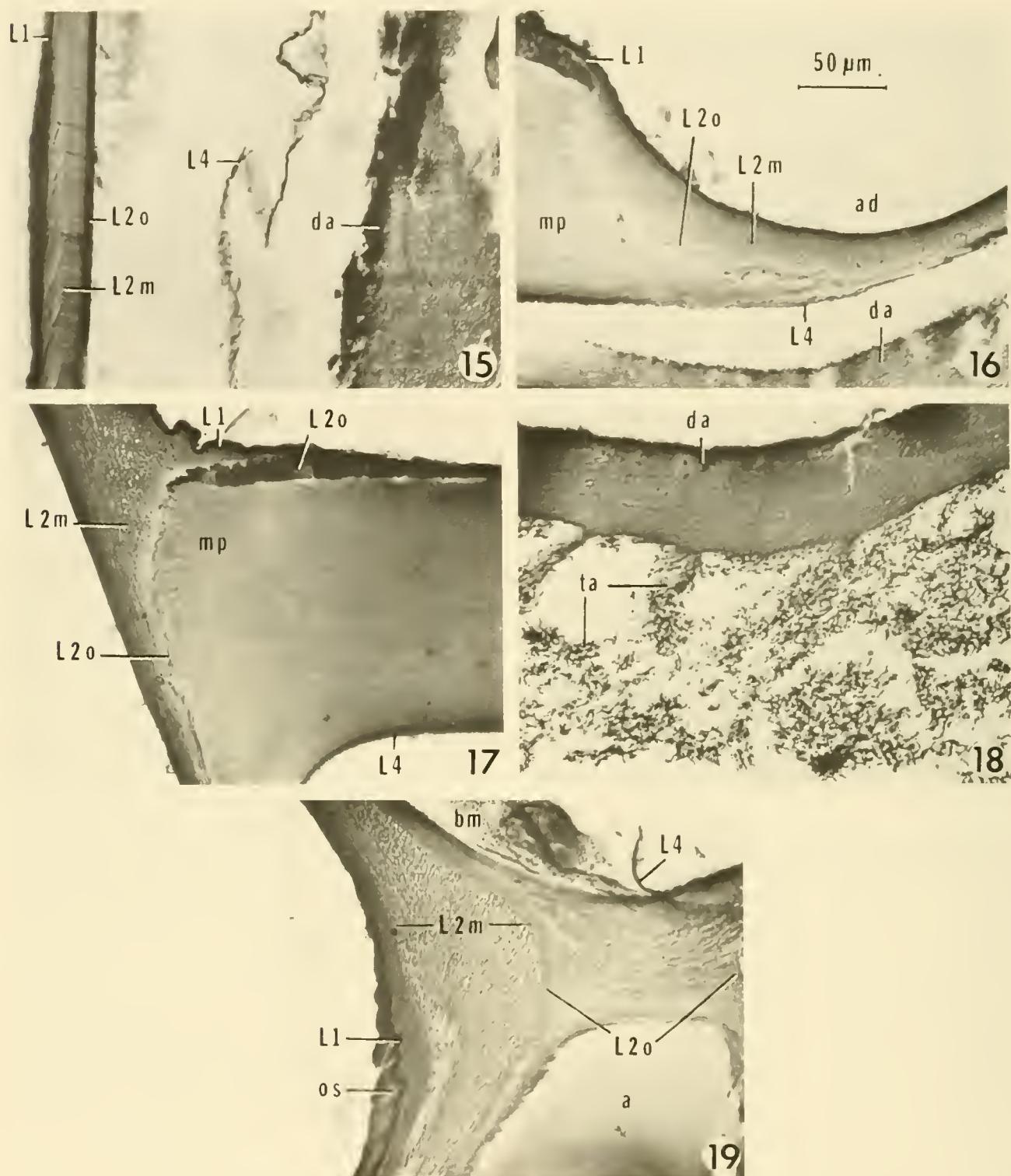
Figures 15–19. Sections of the *Cantharus multangulus* egg capsule. **15.** Wall showing laminae. **16.** Escape aperture adjacent to apical depression. **17.** Escape aperture on side opposite apical depression. **18.** Albumen layers. **19.** Stalk and adhesive. Positions at which photographs were taken are indicated on figure 13. a = adhesive, ad = apical depression, bm = basal mucoid material, da = dense albumen, L1 = orthochromatic first lamina, L2 = second lamina, L2m = metachromatic component, L2o = orthochromatic component, mp = mucoid plug, os = outer surface of L1, ta = thin albumen.

Table 2. Comparative micromorphology of buccinacean egg capsules stained in most cases with toluidine blue (meta = metachromatic, mp = mucoid plug, nr = not reported, ortho = orthochromatic, pre = present, tt = two types of albumen cells in the oviduct).

Species	Width of wall	t1	t2	L3	L4	Layers closing aperture	Layers of albumen	Author
Cantharus multangulus	23 μm	ortho, 1–2 μm	ortho and meta, 21 μm	vestige	meta, 1–2 μm	L1, L2, mp, L4, 210 μm	two meta	this report
Cantharus cancellarius	22 μm	ortho, 2 μm	ortho and meta, 17 μm	vestige	meta, 3–4 μm	L1, L2, mp, L4, 117 μm	two meta	this report
Busycon carica and B. canaliculatum	nr	pre	pre	pre	pre	nr	two	Harasewych, 1978
Nassarius reticulatus	nr	three layers of uncertain relationship mentioned				nr	tt	Fretter, 1941
Buccinium undatum	nr	pre	two fibrous layers	mucoid layer	nr	nr	tt	Fretter, 1941
Ilyanassa obsoleta (L0 pre)	11–22 μm	meta 0.2 μm	pre, 9–10 μm	meta, 1 μm	pre, 60 nm	L1, L2, L3 (mp), L4, 110–150 μm	nr	Sullivan and Maugle, 1984

(figure 13, AD). In the intact capsule, the depression is not obvious when viewed apically. *Cantharus cancellarius* (Conrad, 1846) has similar sculpture on its apical plate (figure 14, AD).

Capsules of *C. multangulus* have a wall in which the fibers appear fused in most regions when viewed with light microscopy. There are three distinct components that appear homologous to three of the four muriccacean laminae: L1, a dense, orthochromatic outer lamina; L2, a mostly homogeneous central lamina, including vacuoles in some regions and fibers in others; and L4, a retaining layer surrounding the albumen (figure 15; table 2). L1 stains intensely and may appear black. L2 may have up to four layered but fused components with the outermost being metachromatic and the innermost orthochromatic. The innermost component, like L1, is intensely stained and may appear black (figure 15, L2o). L2 has somewhat tubular vacuoles in the metachromatic area, especially near the apical depression and where the wall is folded into ridges or spines (figures 16, ad, L2m; 17, L2m). L3, which in many muricaceans is continuous with a mucoid plug in the escape aperture, is not a distinctive feature in the capsule wall (see the following comments concerning the escape aperture). The albumen retaining layer is characteristically wrinkled when it separates from the wall (figure 15, L4).

Albumen occurs in two metachromatic components: a dense portion, broadest near the apical plate, containing short, closely packed fibers with attached, irregular granules, and a thinner, more diffuse portion with coarser fibers and granules, filling most of the lumen (figures 15, da; 18, da, ta). Embryos are positioned in the latter.

The escape aperture is closed by four layers. L1, the outer component, is in continuous contact with the orthochromatic part of L2 (figures 16; 17, L2o). The or-

thochromatic part of L2 is somewhat folded, intensely stained, and may fracture vertically during sectioning. The broadest layer closing the aperture is a metachromatic, mucoid plug lying between the orthochromatic part of L2 and L4 (figures 13, MP; 16, 17, mp). Apically, the mucoid plug lies between L2 and L4 in the homologous position for L3 in muricaceans, but it does not extend to the base of the lumen as a continuous lamina (figure 13). However, above the stalk between L2 and L4, there is some metachromatic mucoid material with chromotropic characteristics similar to those of the apical plug (figures 13, BM; 19, bm). This mucoid material could have been formed at the same time as the plug and would be homologous to L3. L4 is the innermost layer closing the escape aperture.

The stalk and basal plate are formed from L1 and most of L2, while the base of the capsular lumen is formed from the orthochromatic part of L2, some mucoid material, and L4 (figure 19, L2o, bm, L4). The stalk has a core of metachromatic mucoid adhesive (figure 19, a).

Cantharus cancellarius (Conrad, 1846)
(figures 14, 20–23; table 2; USNM 847140)

The macromorphology of the egg capsules of this species was described by Radwin and Chamberlin (1973:110, fig. 8) and D'Asaro (1986a:84, fig. 2). Most median sections of the capsules are cylindrical to vasiform in outline (figure 14). A rounded depression in the apical plate, similar to one observed in *C. multangulus*, is prominent and partially covered by a raised transverse ridge folded toward the escape aperture.

As in *C. multangulus*, much of the capsule wall appears to be composed of fused fibers. Three structural
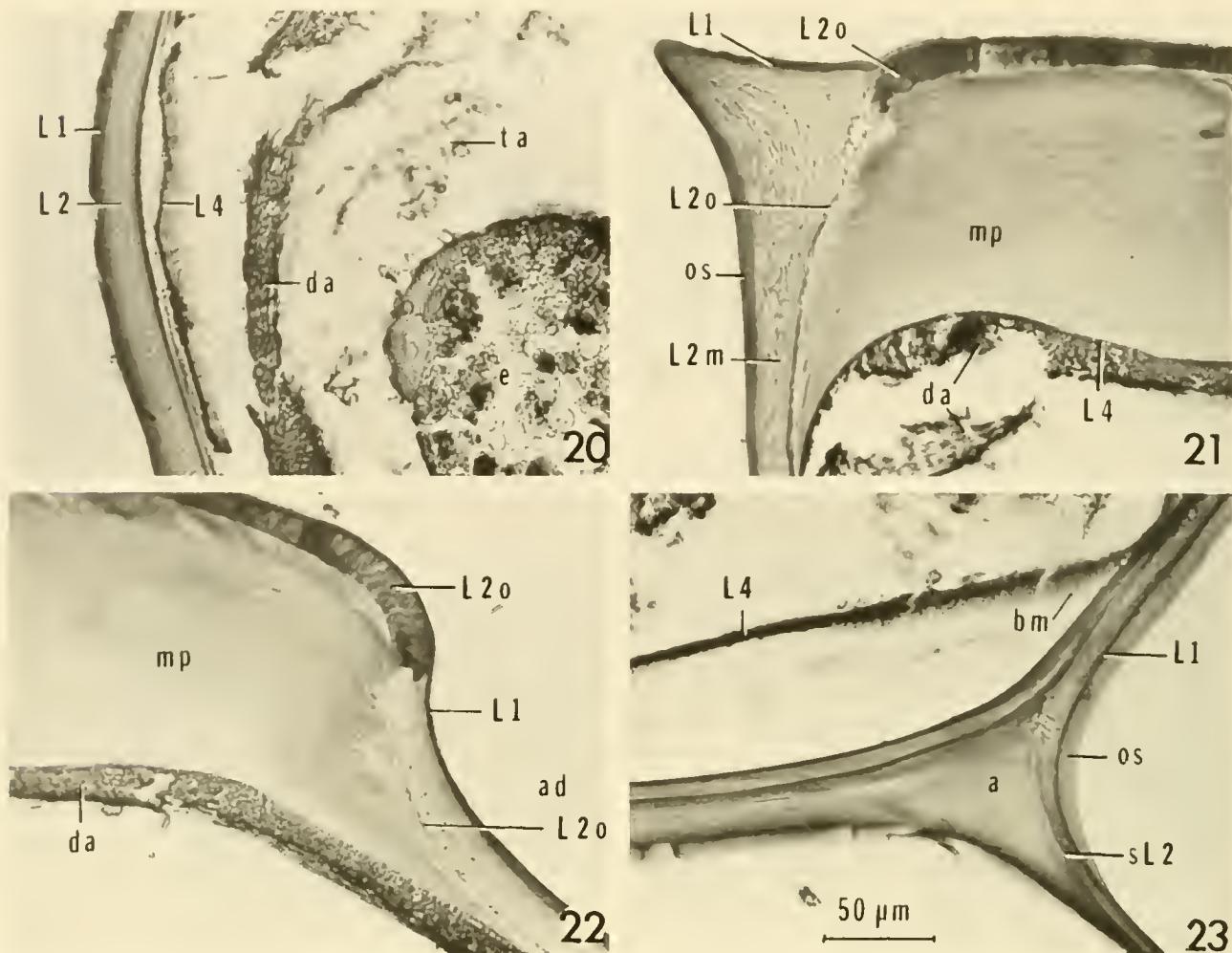
Figures 20–23. Sections of the *Cantharus cancellarius* egg capsule. **20.** Wall showing laminae. **21.** Escape aperture opposite apical depression. **22.** Escape aperture adjacent to apical depression. **23.** Basal plate and adhesive. Positions at which photographs were taken are indicated on figure 14. a = adhesive, ad = apical depression, bm = basal mucoid material, da = dense albumen, L1 = orthochromatic first lamina, L2 = second lamina, L2m = metachromatic component, L2o = orthochromatic component, mp = mucoid plug, os = outer surface of L1, sL2 = outer portion of L2 in the stalk, ta = thin albumen.

laminae, homologous to three of the four muricacean laminae, are present. These are: L1, a very thin, orthochromatic outer lamina; L2, an orthochromatic and metachromatic central lamina with tubular vacuoles; and L4, a metachromatic albumen retaining layer (figure 20; table 1). L1 is often denser on the apical plate. Distinct tubular vacuoles are present in the central portion of L2, especially where ridges exist in the wall and apical plate. Longitudinally directed vacuoles are positioned nearer to the outer surface, while more circularly directed vacuoles are nearer to the inner surface. Apically, where the wall is folded, fibers in the lamina are visible (figure 21). As shown for *C. multangulus*, L3 is not present as a distinct and continuous lamina throughout the whole capsule. The metachromatic albumen retaining layer is extremely thin and can be identified only where it is pulled away from the albumen or the capsule wall and folded to one side (figure 20, L4). Dense metachromatic albumen with fine fibers surrounds more coarsely fibered, less dense albumen in which embryos are positioned (figure 20, da, e, ta).

The escape aperture is closed by four layers arranged in a pattern essentially identical to that of *C. multangulus*. Apically, L1 forms the outermost layer (figures 21, 22). The expanded, orthochromatic part of L2 is the second component. It has vertical folds or fractures (figures 21; 22, L2o). The broadest component is a metachromatic mucoid plug lying between the orthochromatic part of L2 and L4 (figures 21; 22, mp). This plug tapers basally between L2 and L4, but does not extend to the base as a continuous lamina equivalent to L3. There is a layer of similar mucoid material positioned between L2 and L4 at the base of the lumen (figures 14, BM; 23, bm).

Basally, the plate is formed from L1 and most of L2 (figures 14; 23, sL2). Only the orthochromatic, proximal

part of L2 extends across the base, where it, some mucoid material, and L4 form the floor of the lumen. Unlike most specimens of *C. multangulus*, the lumen is separated from the substratum by only a narrow layer of metachromatic adhesive (figure 23, a).

Conus floridanus floridensis Sowerby, 1870
(figures 24, 26–29; table 3; USNM 847141)

Median capsular sections typically have the longitudinal axis angling away from the axis of the stalk and show a slightly irregular outer surface (figure 24). Macromorphology was described by Perry and Schwengel (1955: fig. 360, as *C. spurius atlanticus* Clench, 1942) and D'Asaro (1986a:88, fig. 4).

The capsule wall has three distinct components: L1, a fibrous metachromatic outer lamina; L2, a finely fibered, orthochromatic central lamina; and L4, a thin, metachromatic albumen retaining layer (figure 26; table 3). L1 is very transparent and has fibers circular in cross section. Occasional corrugations mark this lamina, especially near the escape aperture and external ridges (figure 27, L1). Fibers in L2 tend to form a cross-hatched pattern in the upper three quarters of the capsule, but some align with the long axis in the stalk and the base (figures 26–29). Globular structures buried in the fibrous layer occur frequently (figure 27). No homologue of L3 is present as a distinct layer, nor is there evidence that the mucoid plug in the escape aperture is homologous to L3. The albumen retaining layer (L4) is not obviously fibrous. Although this layer is the third in sequence, it is designated as L4, the albumen retaining layer, because its position and probable function appear the same as L4 in Muricacea and Buccinacea.

In this species, only one layer of fibrous, metachromatic albumen is visible (figure 26, al). Granules are attached to the widely separated fibers. Embryos are randomly positioned in the albumen.

The sealed escape aperture is less complex than similar structures formed by muricaceans or buccinaceans. It is lined on its outer surface by L1 and on its inner surface by L4. L2 is replaced by metachromatic, layered mucoid plug with which it interdigitates extensively (figure 27, mp). The degree of interdigitation suggests that L2 and the mucoid plug were formed at the same time.

The stalk is composed of L1 and almost all of L2 from both sides, while the basal plate on each side is composed of L1 and L2 from the same side (figures 28, 29, sL2). A fibro-mucoid, metachromatic adhesive, which may extend into the stalk, attaches the basal plate to the substratum (figure 29, a). Fibers from L2 radiate widely into the adhesive, especially where it extends into the stalk.

Conus jaspideus stearnsi Conrad, 1869
(figures 25, 30–32; table 3; USNM 847148)

When sectioned, the lamellate capsules, described by D'Asaro (1986a:88, fig. 4), appear pointed at the apex with a broad stalk and an escape aperture on one side.
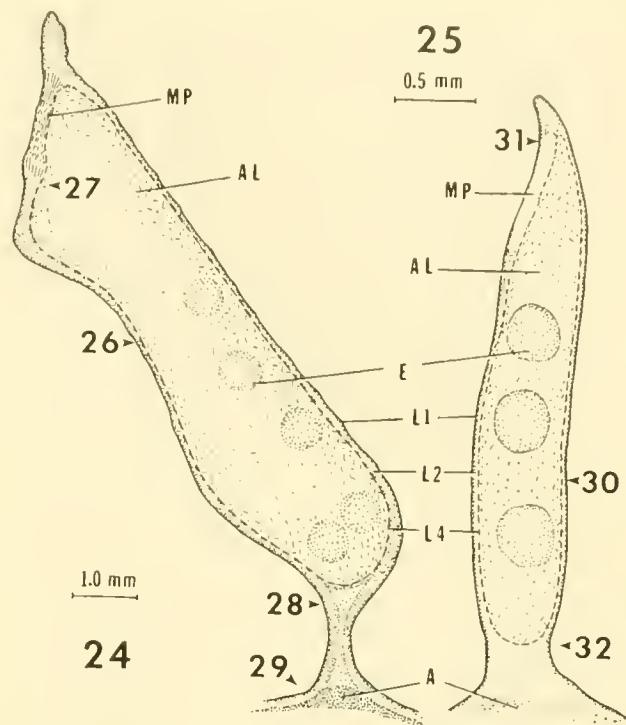

Figure 24. Schematic drawing of a longitudinally sectioned egg capsule of *Conus floridanus floridensis*. **Figure 25.** Drawing, like figure 24, of a *Conus jaspideus stearnsi* egg capsule. Numbers with arrowheads indicate positions at which photographs for figures 26–32 were taken. A = adhesive, AL = albumen, E = embryo, L1 = metachromatic first lamina —solid line, L2 = second lamina—light stipple, L4 = metachromatic albumen retaining layer—broken line, MP = mucoid plug.

In this plane, the basal plate is the widest part (figure 25).

Three laminae were identified: L1, a finely fibered, metachromatic outer lamina; L2, a complex orthochromatic and metachromatic lamina with fibrous and mucoid components; and L4, a metachromatic albumen retaining layer (figure 30; table 3). L1, with circular fibers, is tightly fused to the fibrous portion of L2. Except near the escape aperture and on the stalk, this layer is uniformly corrugated (figures 30; 31, os). L2 has an orthochromatic outer component with coarse, circular fibers (figure 30, L2). The inner component of L2 consists of at least three metachromatic layers of mucoid material containing scattered fibers arranged parallel with the long axis (figures 31, 32, mL2). Of the species studied, only *C. f. floridanus* has a similar arrangement of fibers in mucoid material, and that occurs only in the stalk. No distinct lamina equivalent to L3 is present. L4 may have fragments of albumen fused to its inner surface (figure 32, is).

Albumen in this species is metachromatic and includes scattered transparent spherules and irregular granular material that may form layers (figures 30–32). Embryos are distributed throughout it.
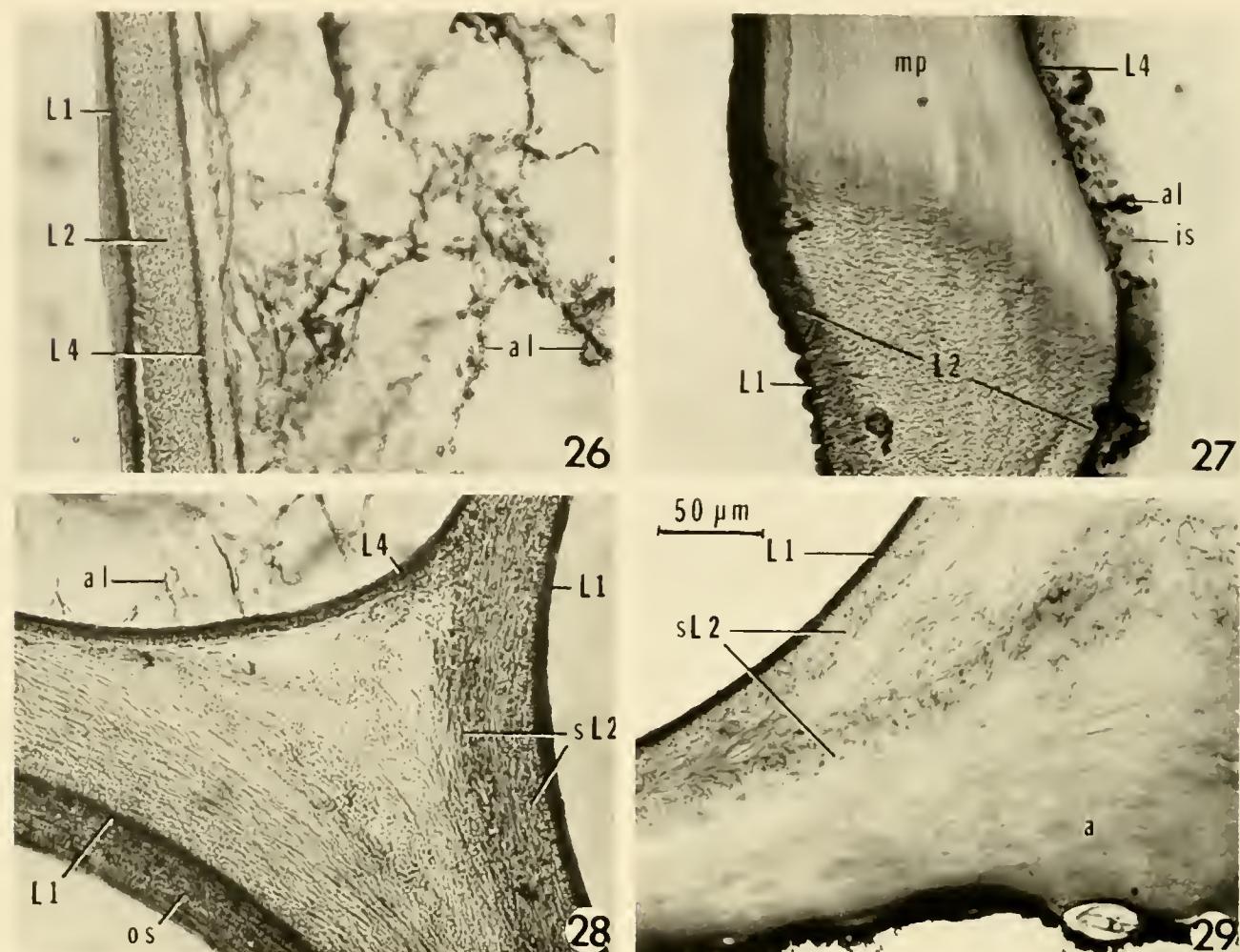
Figures 26–29. Sections of the *Conus floridanus floridensis* egg capsule. **26.** Wall showing laminae. **27.** Escape aperture. **28.** Stalk. **29.** Basal plate and adhesive. Positions at which photographs were taken are indicated on figure 24. A = adhesive, al = albumen, is = inner surface of L4, L1 = metachromatic first lamina, L2 = orthochromatic second lamina, L4 = metachromatic albumen retaining layer, mp = mucoid plug, os = outer surface of L1, sL2 = outer portion of L2 in the stalk.

Table 3. Comparative micromorphology of conid and marginellid egg capsules stained in most cases with toluidine blue (meta = metachromatic, mp = mucoid plug, ortho = orthochromatic, pre = present).

Species	Width of wall	L1	L2	L3	L4	Layers closing aperture	Layers of albumen	Author
Conus floridanus floridensis	49 μm	meta, 5 μm	ortho, 40 μm	not pre	meta, 3–4 μm	L1, mp, L4, 330 μm	one meta	this report
Conus jaspidius stearnsi	25 μm	meta, 2–3 μm	ortho and meta, 22 μm	not pre	meta, 1–2 μm	L1, mp, L4, 114 μm	one meta	this report
Granulina ovuliformis	15 μm		one lamina present			suture in wall	two meta	this report; D'Asaro, 1986
Marginella aureocincta	12 μm		one lamina present			suture?	two meta	this report; D'Asaro, 1986

L1 forms the outer covering of the escape aperture, while the inner lining is L4. A metachromatic, mucoid plug replaces L2 (figure 31, mp). The edges of the mucoid plug are separated from L2 by an interdigitating metachromatic boundary zone, similar but less complex than that of *C. f. floridensis*. None of the scattered fibers in the metachromatic mucoid layers of L2 enter the mucoid plug.

The two outer laminae form the stalk and basal plate, while the base of the capsule is composed of the albumen retaining layer and the inner, mucoid part of L2 (figure 32, mL2). The stalk varies in length; therefore, in some specimens the lumen of the capsule may be nearly level with the substratum. A dense mucoid adhesive is present basally (figure 32, a).

Granulina ovuliformis (Orbigny, 1841)
(figure 33; table 3; USNM 836973)

Macro- and micromorphology of the egg capsules, based in part on eosinophilic features, were described by D'Asaro (1986b:196, figs. 3–5). Because of structural differences, marginellid capsule micromorphology is not describable with reference to Tamarin and Carriker's (1967) system of enumerating capsule laminae.

The simple, pustulate capsules are constructed from an inner component, enclosing two layers of albumen and an embryo, and basement and outer components that sandwich and fuse the previously mentioned structure between them (D'Asaro, 1986b). Because these components were uniformly unstained and did not delaminate during sectioning, the capsule wall is defined as having a single structural lamina of uniform composition, possibly formed by the same portion of the oviduct that produced the layers of L2 in muricaceans and buccinaceans (figure 33, cw). The outer surface of the capsule is coated with metachromatic mucus. No escape aperture with a mucoid plug exists. The point at which the capsule wall fractures at hatching is marked by a distinct metachromatic suture (figure 33, s). Dense granular albumen lies just below the capsule wall, while a less dense component immediately surrounds the single embryo. Both albuminous layers stain metachromatically. The adhesive on the basal layer is not stained (figure 33, a, bl).

Marginella aureocincta Stearns, 1872
(figure 34; table 3; USNM 836974)

Macro- and micromorphology of the egg capsule were described by D'Asaro (1986b:195, figs. 3–5). With application of toluidine blue, all parts of the capsule are metachromatic, except the unstained basement adhesive. The capsule wall does not delaminate and stains intensely to the point of obscuring its layered structure suggesting that, as in *Granulina ovuliformis*, it should be defined as a single structural lamina (figure 34, cw, osw). Distinctive granulations, described by D'Asaro (1986b:195, fig. 3), are obvious on the outer surface. No specific fibrous layer surrounds the albumen. The metachromatic, finely granular albumen occurs in two compo-
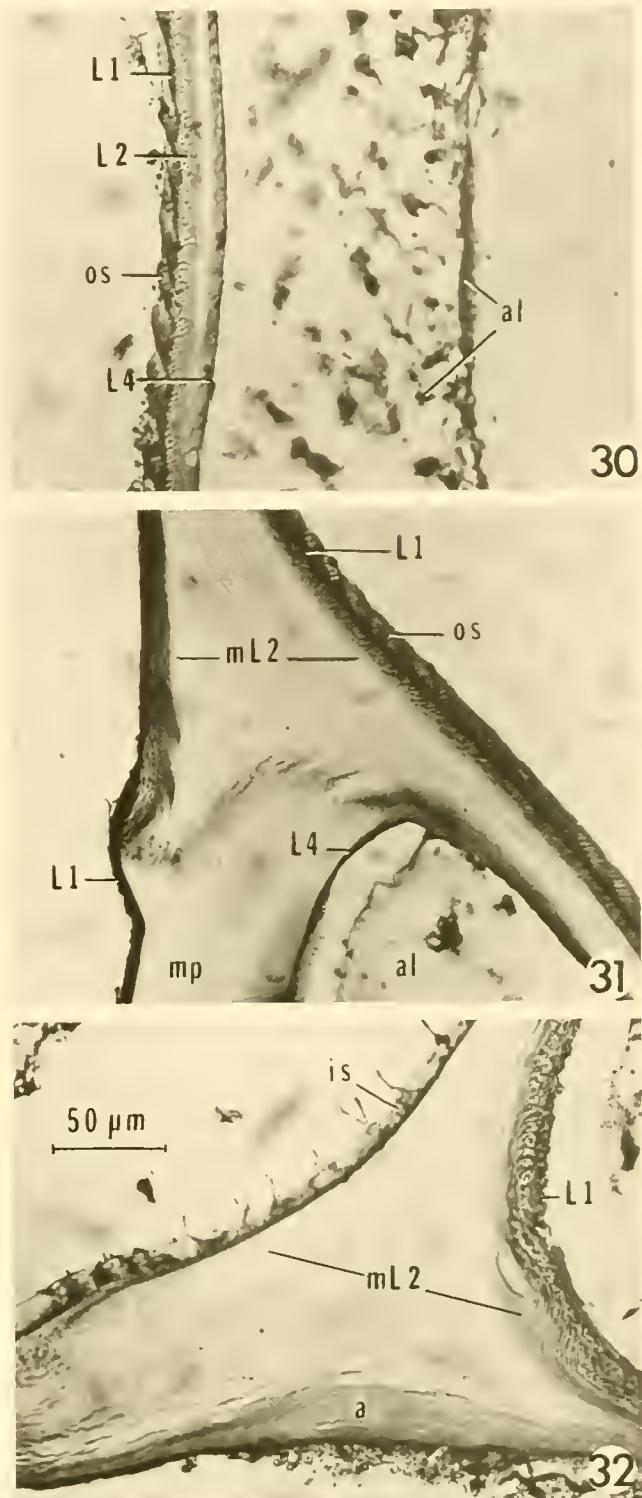
Figures 30–32. Sections of the *Conus jaspideus stearnsi* egg capsule. **30.** Wall showing laminae. **31.** Escape aperture toward apex. **32.** Stalk, basal plate, and adhesive. Positions at which photographs were taken are indicated on figure 25. a = adhesive, al = albumen, is = inner surface of L4, L1 = metachromatic first lamina, L2 = orthochromatic and metachromatic second lamina, L4 = metachromatic albumen retaining layer, mL2 = mucoid component of L2, mp = mucoid plug, os = outer surface of L1.
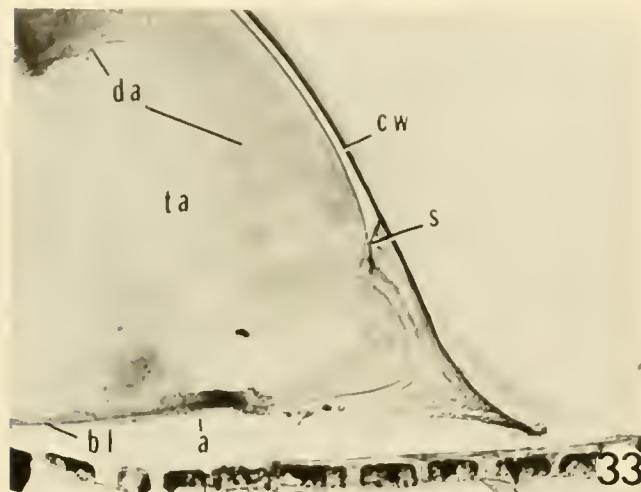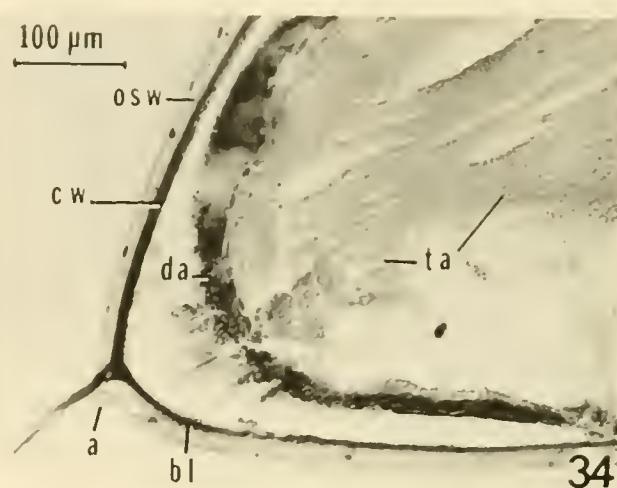
Figure 33. Section of the *Granulina ovuliformis* egg capsule attached to a *Thalassia* leaf. **Figure 34.** Section of the *Marginella aureocincta* egg capsule, a = adhesive, bl = basement layer, cw = capsule wall, da = dense albumen, osw = outer surface of capsule wall, s = suture, ta = thin albumen.

nents, a narrow band of dense material and a more fluid, central zone in which the embryo lies (figure 34, da, ta).

DISCUSSION

Separation of structural laminae by fracturing and toluidine blue staining allows differentiation and identification of homologous components of neogastropod egg capsules. Laminae can be identified in this manner because the fibers of which they are composed appear to have been secreted and chemically bound together during separate phases of assembly. Separate or combined functions related to protection, structural support, release of larvae or juveniles, and albumen retention are inferred for the structural laminae.

Among the neogastropods studied, three microstructural patterns of laminae were identified, each characterizing specific higher taxa. Complex, four-layered capsules with an escape aperture sealed by four layers, including two that are mucoid, were found in nearly all muricaceans and buccinaceans examined. Three-layered capsules having an escape aperture sealed by three layers, including one that is mucoid, were found in the Conidae. Uncomplicated, single-layered capsules that may only have a suture in the wall to facilitate hatching appear to be characteristic of the Marginellidae.

Muricacea and Buccinacea are species-rich taxa having family or species-specific egg capsule morphologies with a final shape that results from a molding process in the ventral pedal gland (Ankel, 1929; Gruber, 1982; Sullivan and Maugel, 1984). Micromorphological similarities suggest that oviducal mechanisms common to both superfamilies are used to construct structural laminae that serve the same respective functions in these taxa (tables 1, 2). Some species may add additional nonstructural layers in the ventral pedal gland (table 2, L0; Sullivan and Maugel, 1984).

Protection (sealing the fibrous wall) appears to be a

function of the outer structural lamina, L1. In most species, L1 is thin (5 µm or less), usually dense and finely fibered, and reflects the final shape (corrugations and ribbing) imparted by the ventral pedal gland (Gruber, 1982; Sullivan and Maugel, 1984). L1 seals the surface of the whole capsule including the escape aperture, but not the basal plate in contact with the adhesive. Since the contents of some prosobranch egg capsules are axenic but not bacteriostatic (Lord, 1986), the fine structure of this lamina could serve as a physical barrier to invasion by microorganisms, especially in species with a vacuolated and fluid-filled L2. (The basal adhesive may also serve as a barrier.) In *Urosalpinx cinerea*, L1 is thick with separated fibers, but the interstices are filled with dense mucus (Tamarin and Carriker, 1967). L1 could also serve as a reactive substrate during the molding and hardening process in the ventral pedal gland which fixes the capsule in its final shape (see Gruber, 1982 and Sullivan and Maugel, 1984).

L2 comprises the internal skeleton of the capsule wall in all neogastropod taxa studied except Marginellidae, which has a single structural lamina (tables 1–3). In some taxa, extensive cross-linkages between the protein fibers form a homogeneous L2. In others, there are dense homogeneous zones on inner and outer surfaces gradually separating into directionally oriented fibers forming most of the lamina. In ribs or other sculpture, these fibers are loosely packed. The homogeneous zones, in addition to skeletal support, could provide another physical barrier to invasion by microorganisms.

In Muricacea and Buccinacea, L2 may have fibrous components with different axial orientation often described as separate layers (Fretter, 1941; Gruber, 1982). Resistance to delamination and cohesiveness suggest that these layers were constructed from the same capsular protein during a continuous process; thus, they should be described as parts of a single capsular lamina. If all similar fibrous components and contiguous homogeneous

zones from previously described egg capsules of these superfamilies are viewed in this manner (as organized in tables 1, 2), then more meaningful comparisons between taxa can be made.

L3 is distinct in most muricaceans and buccinaceans and appears to be a mucoid extension of the apical plug, a part of the hatching mechanism (tables 1, 2). In both species of *Cantharus*, L3 is not present in most of the capsule wall; however, the mucoid plug in the escape aperture tapers gradually into the wall in a homologous position. There is also mucoid material with chromotropic characteristics similar to the apical plug in a homologous basal position suggesting that a thin layer of L3 mucopolysaccharide may be present throughout the wall but could not be identified with the histological technique applied. In the egg capsule of *Eupleura caudata etterae*, which was described by Gruber (1982: fig. 14), the singular mucoid plug extending as a layer into the capsule wall and surrounding the lumen can be described as L3. Lying between the outer structural layers and L3 in *E. c. etterae*, is another layer (Gruber's sixth layer). The position of this layer, in contact with the equivalent of L2 and surrounding the outer edge of the mucoid plug formed by L3, and its composition suggest that it is homologous with the first mucoid plug in *Chicoreus florifer dilectus* (table 1).

L4, the albumen retaining layer, is the primary lamina in muricaceans and buccinaceans completely surrounding albuminous fluids and embryos (tables 1, 2). Often it is not reported in the literature, perhaps because it is 4 μm or less in thickness and usually bound tightly to other components. A function of the layer could be to prevent nonrefractory albumen from mixing with refractory capsular proteins when the outer structural laminae are assembled by the ciliary mechanism Fretter (1941) described.

Albumen in egg capsules of muricaceans and buccinaceans is stratified to some degree at oviposition (tables 1, 2). This was rather obvious in capsules of *Chicoreus florifer dilectus*, which had a core of dense albumen, free of embryos, that was structurally different from the surrounding, less dense material. More typically in other species, the core albumen contained the embryos. Different layers of albumen in newly deposited capsules suggest that two or more kinds of albumen producing cells exist in the oviducts of the species studied, as Fretter (1941) has demonstrated for several neogastropods.

Muricaceans and buccinaceans have structurally similar barriers closing the escape apertures, which are five to nine times as thick as the capsule wall (tables 1, 2). The increased thickness of the less refractory mucoid plugs possibly serves to prevent premature hatching of a capsule. In muricaceans, no fibers from the more refractory parts of L2 extend into the mucoid plugs. During sectioning, mucoid plugs in the escape aperture fractured across the width of the capsule wall, while the more refractory parts of the capsule delaminated lengthwise. Boundary laminae in the wall (L1 and L4) appear to hold the mucoid plugs in position.

Conid egg capsules are less complex than those of the Muricacea and Buccinacea and contain smaller structural fibers, usually embedded in a mucoid component. The capsule wall has two laminae (L1 and L2) and an albumen retaining layer (L4). Rather than having ribbon-like fibers in the laminae (see Flower *et al.*, 1969, for a discussion of fiber ultrastructure), there are very fine, short, and folded or twisted fibers that overlap into a cross-hatched pattern. A singular mucoid plug lying between the outer laminae, L1, and the albumen retaining layer, L4, and interdigitating extensively with the fibrous middle lamina seals the escape aperture. Extensive interdigitation would require simultaneous formation of L2 and the mucoid plug. There is no evidence in the conids studied of a lamina equivalent to L3 associated with the mucoid plug. These differences in micromorphology suggest that important differences in oviducal structure and function exist between conids and muricaceans and buccinaceans.

Pustulate marginellid egg capsules are microstructurally the least complex of the taxa studied, and differ markedly from capsules of other neogastropods. Each is constructed of three homogeneous components fused almost indistinguishably into the others to form a capsule in which the parts do not delaminate during sectioning. Resistance to delamination and a uniform response to toluidine blue suggest that only one protein was used to form the capsule wall. There is no complex escape aperture, but in many marginellids it is possible to identify a preformed suture at which the capsule will break during hatching. The suture is visible at one end and on the sides, which corresponds exactly to the position where the capsule wall breaks during hatching. These features also suggest that the structure and function of the marginellid oviduct is different from that of the major superfamilies studied.

Although this study does show that there are micromorphological features common to the egg capsules of some prosobranch taxa, it does not provide clear evidence that can be used to explain exactly how capsules are formed in the oviducal glands. It can be inferred that L4, the albumen retaining layer, is deposited around the albumen and embryos to hold them in a central position while the more refractory parts of the capsule are formed. It can also be inferred that for most species the remaining parts of the process involve sequential deposition of structural laminae, as Fretter (1941) described for *Nassarius reticulatus*, with L3 and formation of the innermost mucoid plug being the second part of the process. The third part of assembly would involve formation of the main structural lamina, L2, and the outer mucoid plug. L1 would be the last structural lamina added. Sculpturing, hardening, addition of nonstructural layers, and attachment with an adhesive are functions of the ventral pedal gland (Sullivan and Maugel, 1984).

ACKNOWLEDGEMENTS

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Two New Species of *Metula* (Gastropoda: Buccinidae) with a Description of the Radula of the Genus

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ABSTRACT

Two species of *Metula* H. and A. Adams, 1853, lack a radula, and it is very small in a third species. The morphology of the teeth is significantly different from that in *Pisania*, and the two genera are probably not closely related. *Metula crosnieri* new species, from 400–450 m off SW Madagascar, is a large, broad species, with very convex whorls and a deep suture. *Metula africana* new species, from the deep continental shelf off West Africa, is considered the descendant of the Mediterranean Pliocene *M. mitraeformis* (Brocchi, 1814). This lineage cannot be taken as evidence for Mediterranean–Indo-Pacific connections in the lower Pliocene as claimed by Grecchi (1978).

INTRODUCTION

The chequered taxonomical history of the generic name *Metula* H. and A. Adams, 1853, has recently been stabilized by Emerson (1986), who clarified the identity of its type species, *Buccinum clathratum* Adams and Reeve, 1850. Additional information was provided by Beu and Maxwell (1987).

The familial position of the genus has been the subject of a controversy between Ponder (1968, 1973) and Cernohorsky (1971). Ponder (1968) described the anatomy of *Ratifusus* Iredale, 1919, and *Iredalula* Finlay, 1927; he concluded that their peculiar glandular mid-esophagus as well as other features of the anterior alimentary canal justified their inclusion in the family Colubrariidae, which he considered to be anatomically distinct from the Buccinidae. Cernohorsky (1971) regarded the presence of a vestigial radula in *Ratifusus* and *Iredalula* to indicate placement in the Buccinidae, since the species of Colubrariidae have no radula at all, and he suggested a placement in the buccinid subfamily Pisaniinae. This view has been accepted by most subsequent authors dealing with *Metula* (Olsson and Bayer, 1972; Kilburn, 1975; Houbrick, 1984; Emerson, 1986), who apparently overlooked Ponder's (1973) refutation of Cernohorsky's point of view. Ponder (1973) confirmed that *Ratifusus*, *Iredalula*, and *Colubraria* shared the same anatomical characters that separate them from the Buccinidae, and commented on the radular differences: "It thus appears that some Colubrariidae have lost the radula and that it is

relatively small or vestigial in the remainder. It is possible that the whole *Metula-Ratifusus* series discussed by Cernohorsky (1971) belongs in the Colubrariidae as they all have similar shell features" (Ponder, 1973:328).

The family Colubrariidae is treated as a synonym of Buccininae by Ponder and Warén (1988), while Beu and Maxwell (1987) recognize a subfamily Pisaniinae, where they include *Metula*, *Colubraria*, and a number of other genera.

The purpose of the present paper is to provide a name for the West African species that has been known in the recent literature as *Metula clathrata* Adams and Reeve, and to describe another new *Metula* from the upper continental slope in the Mozambique channel. Several additional Indo-Pacific species of *Metula*, now under study, can be distinguished only on the basis of their protoconch, which has already been emphasized by Altena (1949) as a taxonomical character.

SYSTEMATICS

The radula of a species of *Metula* is figured here for the first time (figure 1). It is very small for a buccinid (ribbon 25 µm wide; central tooth 6.5 µm wide, lateral teeth 12 µm wide) and very similar to the radulae of *Ratifusus* and *Iredalula* figured by Ponder (1968): the central tooth has a narrow arched basal plate with 3 long, slender, and equal cusps; the lateral teeth also have a narrow basal plate and 3 long slender cusps, the outermost one being longest.

A radula has been looked for, but not found in *Metula amosi* Vanatta, 1913, and *M. cumingi* (Adams, 1853); several specimens were examined in each case by A. Warén (personal communication). I do not consider presence or absence of this very reduced radula to be of generic importance.

The radula (figure 2) of *Pisania striata* (Gmelin, 1791), type species of *Pisania*, is 150 µm wide; it differs in having a central tooth with a large square basal plate and 5 short and broad cusps, the outermost 2 being smaller; the lateral teeth are more strongly built, with 3 unequal cusps.

In view of the small variation of radular types in buc-

cinids, this difference is remarkable and probably indicates that the two genera are not closely related. Whatever rank (subfamily or tribe) the *Pisania* group is given in Buccinidae, additional research is needed before the *Colubraria* group is considered a mere synonym of it.

DESCRIPTIONS

[For a diagnosis of the genus see Altena (1949) as *Antemetula*.]

Metula crosnieri new species
(figures 3–5, 9)

Description: Shell solid, fusiform, consisting of 2.5 protoconch and 6.2 teleoconch whorls. Spire high, body whorl comprising 64% of total shell height. Protoconch (figure 9) with large nucleus of two smooth convex whorls abruptly demarcated from teleoconch. Teleoconch whorls convex, without sutural ramp, with deeply impressed suture. Sculpture of raised spiral cords and curved opisthocline axial ribs; cords and ribs producing beaded intersections and pitted intervals. Eight spiral cords on spire whorls; 4 minor, intermediate cords on penultimate whorl; about 18 cords above periphery of body whorl, principal and secondary cords alternating rather regularly, and 33 cords below periphery, of which about 15 are set close together in siphonal region. Axial ribs about equal in strength to spiral cords on spire whorls; weaker on penultimate whorl, with main sculpture being spiral on body whorl. In addition to axial ribs, several incremental scars are obvious, especially on body and penultimate whorls. Aperture ovate; inner lip thin, smooth, adherent to body whorl, thicker in columellar region; outer lip bearing 12 very weak teeth that do not correspond with position of external spiral cords; two most apical teeth slightly stronger. Peristome thickened, forming broad varix, also covered by spiral cords. Siphonal canal long, broad, widely open, and recurved. Fasciole indistinct.

Colour light tan, with a very indistinct darker spiral band at periphery of body whorl; incremental scars lighter; aperture white.

Dimensions of the holotype: Height 51.3 mm, width 19.4 mm; height of the aperture 24.5 mm, width 8 mm; height of the body whorl 33 mm.

The largest paratype is 55.4 mm high.

Type locality: Mozambique channel, SW Madagascar, off Baie de Fanemotra, 22°15′S, 43°05′E, 470–475 m.

Type material: Holotype and paratype 1 (MNHN) from the type locality, collected by A. Crosnier, Dec. 2, 1973 aboard R.V. "Vauban"; paratype 2 (MNHN), Mozambique channel, SW Madagascar, 22°17′S, 43°04′E, 400–450 m, collected by R. v. Cosel, Nov. 30, 1986 aboard trawler "Mascareignes III".

Distribution: Known only from the type material, off SW Madagascar.
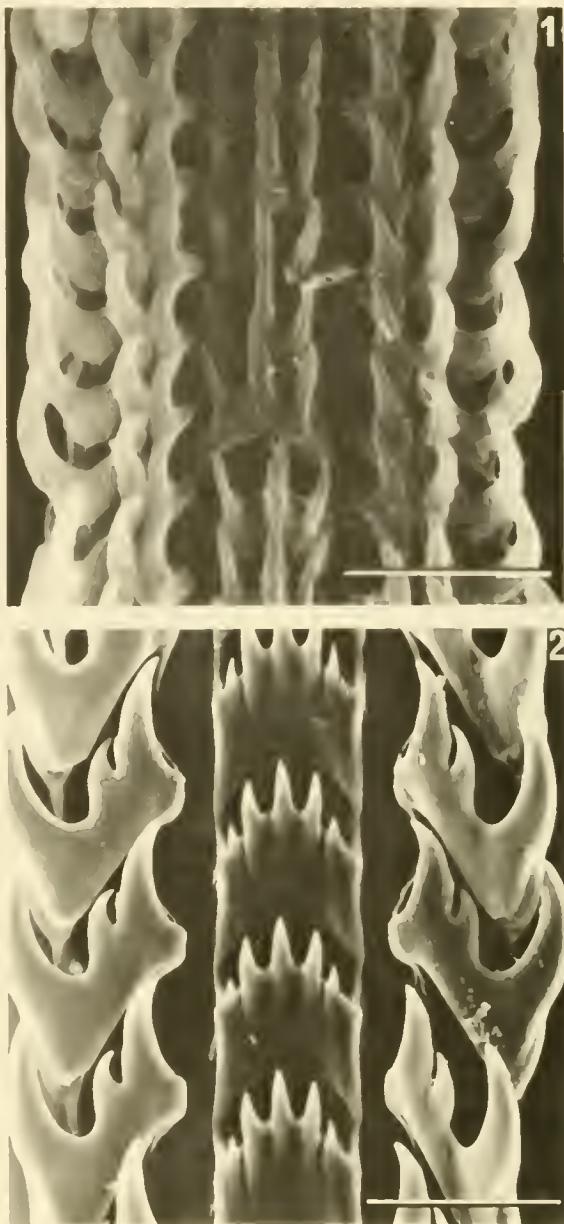
Figures 1, 2. Scanning electron micrographs of radulae. **1.** *Metula africana* new species, scale bar 10 μm. **2.** *Pisania striata* (Gmelin, 1791), scale bar 50 μm.

Remarks: *Metula crosnieri* has remarkably convex whorls and a deep suture when compared with its congeners. The protoconch (figure 9) indicates non-planctotrophic larval development. The combination of these two characters distinguishes it from all known Indo-Pacific *Metula*.

In the Atlantic, *Bartschia significans* Rehder, 1943, type species of *Bartschia* Rehder, 1943, has even more convex whorls, and a multispiral protoconch. I cannot find characters other than the convexity of the whorls that sharply distinguish *Bartschia* from *Metula*, and conclude that *Bartschia* should be considered at most a subgenus of *Metula*.

I am naming this species after my colleague Alain Crosnier, who first collected it during a survey of deep water shrimp populations off Madagascar.

Metula africana new species
(figures 1, 6–8, 10)

Metula clathrata Knudsen, 1956:39, plate 1, figure 1; non *M. clathrata* (Adams and Reeve, 1850).
non *Metula knudseni* Kilburn, 1975:592 (replacement name for *Buccinum clathratum* Adams and Reeve, 1850; see Emerson, 1986).

Description: Shell solid, fusiform, consisting of 7 teleoconch whorls. (Protoconch of holotype partly broken, on a paratype consisting of large nucleus and 1.5 smooth convex whorls, figure 10.) Teleoconch whorls convex, with faint but distinct sutural ramp on early whorls; ramp indistinct on penultimate whorl, body whorl evenly convex. Teleoconch sculpture of raised spiral cords and slightly curved opisthocline axial ribs; intersections distinctly beaded in sutural ramp area, only slightly nodulous below ramp. Spiral and axial sculpture of similar strength on early whorls; later spiral sculpture gradually dominates. Nine primary spiral cords per whorl on spire whorls, first (adapical) and third cords stronger, limiting sutural ramp. Fine spiral threads present between cords on penultimate and body whorl, several eventually developing into secondary spiral cords, with one present in sutural ramp area of body whorl. About 22 primary cords below periphery of body whorl, plus another 10 in siphonal area. Incremental scars distinct; growth lines very distinct between axial ribs. Aperture ovate, narrow. Inner lip thin, smooth, adherent to body whorl, thicker in columellar region. Outer lip regularly convex, bearing small teeth that correspond at least partly with position of spiral cords on peristome; a group of 5 teeth forms a small callus in apical portion of outer lip, delimiting small anal canal. Peristome forming a thickened varix, over which spiral sculpture extends. Siphonal canal short, narrow, open, only slightly recurved.

Ground colour of shell beige cream, with 3 brown spiral bands; 3 adapical cords brown, interval between them beige cream. Below, uniformly beige band extends over next 2 spiral cords, occupies central position on spire whorls. Darkest band occupies next 4 spiral cords and intervals between them; this band occupying suprasutural position on spire whorls, and a central position on body whorl. Below brown band a second beige band extends over 4 spiral cords; next 2 cords brown, with brown colour fading towards base of shell. Aperture cream colored.

Dimensions of the shell: Height 54.5 mm, width 17.5 mm; height of the aperture 27 mm, width 7 mm; height of the body whorl 35 mm.

Type locality: Off Saint Louis, Sénégal, in 300–600 m.

Type material: Holotype (MNHN), paratype 1 (MNHN) and paratype 2 (AMNH 198755), all from the type locality, collected by M. Pin on the trawler "Louis Sauger".
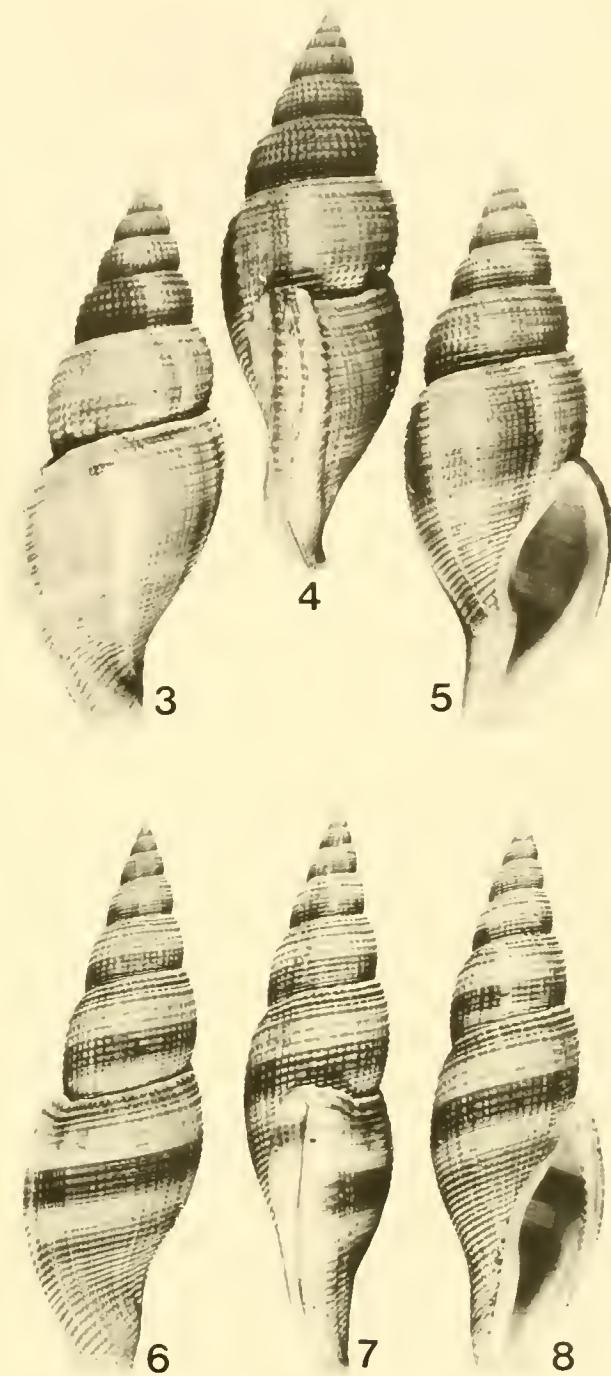
Figures 3–8. Back, side, and front views. **3–5.** *Metula crosnieri* new species, holotype, 51.3 mm. **6–8.** *Metula africana* new species, holotype, 54.5 mm.

Other material examined: SENEGAL: off Saint Louis, "deep water", 4 shells (MNHN, leg. M. Pin), 10 shells (coll. M. Pin, Dakar); IVORY COAST: off Abidjan, 1 shell, coll. Marche-Marchad (MNHN), and 1 shell, P. Le Loeuff coll. (MNHN); EQUATORIAL GUINEA: Atlantide Sta. 120, 02°09′N, 09°27′E, 250–850 m, 1 specimen
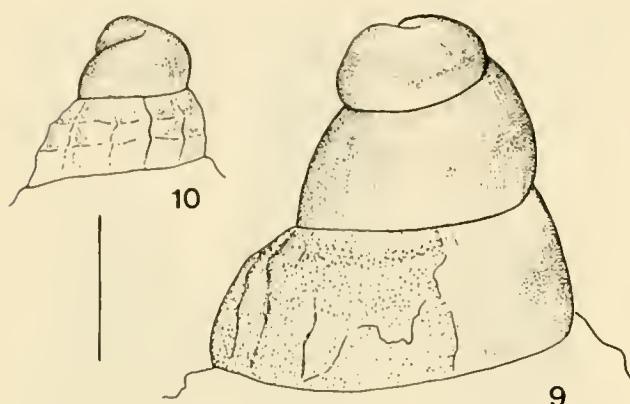
Figures 9, 10. Protoconchs. 9. *Metula crosnieri*. 10. *Metula africana*. Scale line 1 mm.

(Knudsen, 1956) (ZMC); CONGO: West of Pointe-Noire, 100 m, 1 shell, A. Crosnier coll. 1962 (ANSP 333810).

Distribution: Deep continental shelf and upper slope of West Africa, from Senegal to Congo.

Remarks: *Metula africana* has been figured three times in the literature: by Knudsen (1956: plate 1, figure 1) under the name *Metula clathrata*; by Emerson (1986: figures 4, 5) as *Metula* sp.; finally by Kaicher (1987: card 4851) as *Metula* sp. I refer to Emerson (1986) who reviewed the nomenclature of this West African *Metula* and concluded that it represents a new species.

The protoconch (figure 9) indicates non-planctotrophic larval development.

There may be clinal variation in adult size along the West African coast: The 18 shells examined from Senegal have a mean height of 41.7 mm; the 2 shells from Ivory Coast, although fully adult, measure 32 and 36 mm; that from Equatorial Guinea is 30.6 mm high, and that from Congo 25.5 mm.

The tiny rachiglossate radula (figure 1) was prepared from the specimen taken during the Atlantide expedition (ZMC).

The close connection between Mediterranean Pliocene and Recent West African marine faunas has been demonstrated in a number of paleontological papers (for recent reviews see Ruggieri, 1967; Marasti and Raffi, 1979; Sabelli and Taviani, 1984). With a single species of *Metula* present in the Pliocene of Italy and a single Recent species in West Africa, it is reasonable to assume that *Metula mitraeformis* (Brocchi, 1814) (for figures and references see Pelosio, 1966) is the direct ancestor to *M. africana*. I have examined material of the fossil species and found it to differ from the Recent one by its much weaker axial sculpture, which on the body and penultimate whorls is limited to growth lines. In *M. mitraeformis*, there is a very broad sutural ramp that extends over the adapical third or half of early teleoconch whorls, and becomes obsolete on the penultimate and body whorls; the siphonal canal is also broader.

Because he was mistaken about the identity, type lo-

cality, and distribution of *M. clathrata*, Grecchi (1978) speculated that the presence of its presumed ancestor *M. mitraeformis* in the Mediterranean Pliocene was an indication of Mediterranean–Indo-Pacific connections in the lower Pliocene after the Messinian salinity crisis. With *M. clathrata* now known to be a West American species distinct from *M. africana*, the history of the *M. mitraeformis–africana* lineage can not be taken as an indication of such connections. This lineage probably has an Eastern Atlantic history dating to the Miocene; although the Neogene West African fossil record is lacking, it is far more probable that *M. mitraeformis* reinvaded the Pliocene Mediterranean from West Africa rather than from the Indo-Pacific through unproven maritime connections.

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A New Species of Intertidal *Terebra* from Brazil

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ABSTRACT

Terebra imitatrix new species is described from northern Brazil and compared to morphologically similar species of *Hastula*. The three known terebrid feeding types are briefly reviewed. Dissection of the foregut of this new species revealed characters that overlap two of the major feeding types.

Key words: Gastropoda; Terebridae; *Terebra*; anatomy; Brazil.

INTRODUCTION

While compiling distributional records of the West Atlantic *Hastula cinerea* species group, the junior author located an unidentified lot of 23 specimens from Brazil in the Academy of Natural Sciences of Philadelphia (ANSP 299957). These specimens were compared to the known terebrids from the Atlantic and were found to belong to a distinct undescribed species. An additional lot of the same species was subsequently found in the American Museum of Natural History (AMNH 129280). Matthews *et al.* (1975:99, fig. 31) in their treatment of *Hastula cinerea* describe and illustrate a protoconch consistent with this new species. The Brazilian specimens of *Hastula salleana* (Deshayes, 1859) figured by Rios (1970: 123, pl. 47, 1975:127, pl. 38, fig. 560, 1985:131, pl. 45) are probably referable to this new species, but the figured specimen was unavailable for examination. This paper describes this new species and compares it with morphologically similar species of *Hastula*. A description of the foregut anatomy reveals that it does not conform to any of the three known feeding types, which are reviewed herein.

MATERIALS AND METHODS

Only shells possessing 10 or more teleoconch whorls and with intact protoconchs and apertures were measured with Vernier calipers. All dissections were made under a Wild M-5 dissecting microscope and line drawings made with the aid of a camera lucida. Description and discussion of the anatomy is limited to the foregut due to poor preservation in the upper whorls. Anatomical and protoconch measurements were made with an ocular micrometer and converted to millimeters. Terminology follows that of Miller (1970, 1971). Two preserved but completely retracted adult specimens of the new species (ANSP 299957), *Hastula maryleeae* Burch (UF 113539) and *Hastula salleana* (Deshayes) (UF 48197, 113540), were dissected from each lot. Two dried-in specimens of *Hastula maryleeae* Burch (T. Bratcher collection) were rehydrated in a weak solution of potassium hydroxide, transferred into water, and dissected. The radular sac was extracted and dissolved in a weak solution of potassium hydroxide. Radular teeth were individually mounted on scanning electron microscope specimen stubs covered with double-sided tape. Micrographs were made with a Hitachi 5-415A scanning electron microscope.

Repositories of examined specimens are indicated by the following abbreviations:

AMNH   American Museum of Natural History
ANSP   Academy of Natural Sciences of Philadelphia
UF   Florida Museum of Natural History

SYSTEMATICS

Family **Terebridae** Mörch, 1852
Genus *Terebra* Bruguière, 1789

Terebra imitatrix new species
(figures 1–6, 8, 9, table 1)

Description: Shell (figures 1–3, 6) medium in size, broadening anteriorly; color variable, ranging from banded, or cream, to purplish-brown; teleoconch whorls 10–12; sides flat to slightly convex. Protoconch whorls 1.5–2.0; glassy, transparent (figure 6). Axial sculpture of close-set, recurved ribs of variable strength, generally distinct near the suture, becoming obsolete anteriorly; major axial ribs 34–57 ($\bar{x}$ = 41.6) on the penultimate whorl. Spiral sculpture of very faint microscopic incised lines most distinct in the intercostal spaces on the upper whorls, obsolete on later whorls, rarely crossing the axial ribs; spiral rows of pits absent. Last whorl with obsolete axial ribs and spiral incised lines; color pattern variable, typically of five diffuse color bands: one white pre-sutural band usually with distinct brown spots that become obsolete toward apertural lip, one broad bluish-black zone at shoulder, one pinkish band at periphery, one purplish-
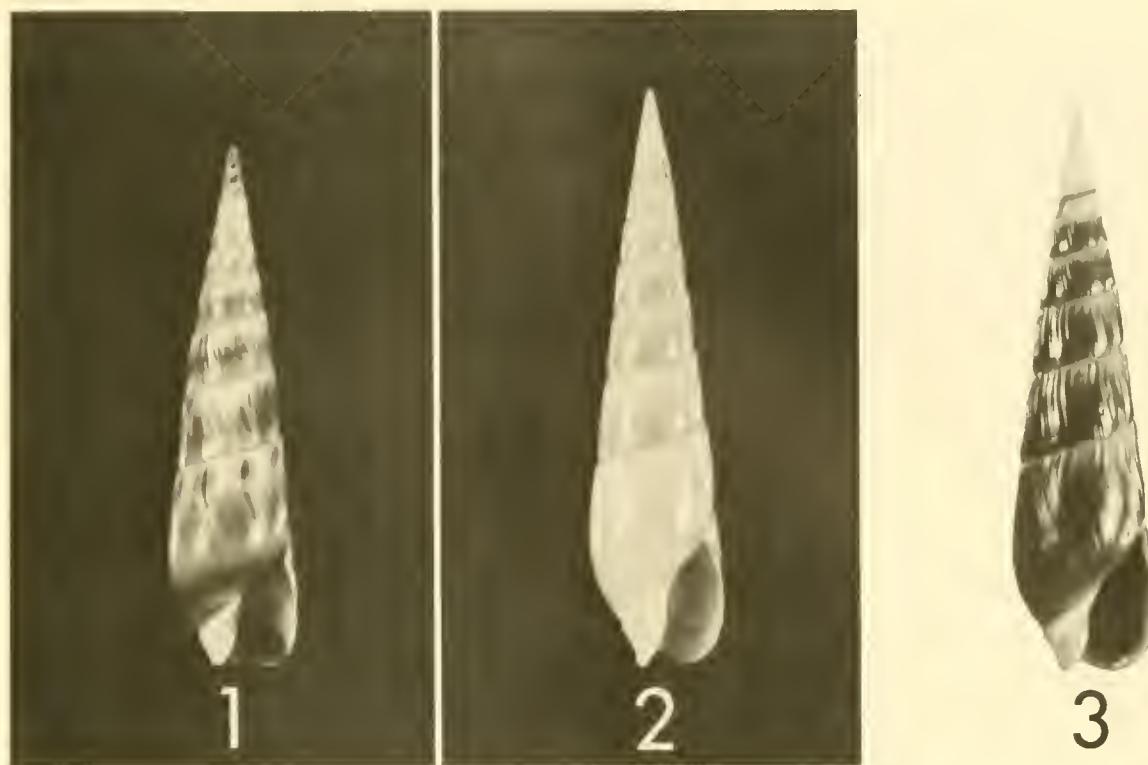
Figures 1–3. *Terebra imitatrix* new species. **1.** Holotype, ANSP 299957 (27.5 mm shell length). **2, 3.** Paratypes, ANSP 369293, all from Rio Grande do Norte, Brazil, sand island at mouth of the inlet at Areia Branca.

brown band below periphery, and one white basal zone. Columella brown, centrally concave and slightly recurved; rounded rib present on anterior edge. Parietal callus thin, transparent to light brown. Fasciole white to bluish-gray with distinct white rib. Anterior siphonal notch moderately broad, straight. Aperture light to dark brown with white band.

External anatomy: Animal cream-colored with no apparent pattern in alcohol-preserved specimens. Operculum corneous, small, thin. Eyes on short, broad eyestalks. Labial tube large, spoon-shaped (figure 4). Anterior end of labial tube terminating in thick muscular lips bounding mouth slit; well-developed sphincter lacking.

Foregut anatomy: Labial cavity large, dominated by massive (3.7 mm), extendable, muscular organ (accessory feeding apparatus; Miller, 1970, 1971) that tapers anteriorly; muscular organ with two rows of papillae on ventral side (figure 4); attached posteriorly to the left side of the cephalic hemocoel by connective tissue; retractor muscle large, originating in foot below and slightly posterior to anterior siphon, passing through cephalic hemocoel. Buccal tube muscular, short (0.9 mm), tapering anteriorly. Buccal cavity small (0.6 mm), rounded. Pre-ganglionic esophagus enters buccal mass posteriorly (figure 4). Salivary glands not located. Radular sac blade-shaped, small (0.8 mm). Radular caecum (0.4 mm) with well-developed groove running posteriorly, two distinct

bulbs anteriorly (figure 5). Radular organs attached to right side of anterior portion of buccal cavity by very short duct (0.1 mm). Two rows of radular teeth situated obliquely in radular sac and caecum (figure 5). Radular teeth about 30; 0.1–0.2 mm in length, slightly curved, not barbed (figures 8, 9). Poison gland long (6.2 mm), extremely convoluted, entering right side of buccal cavity slightly behind radular sac (figure 5). Poison bulb small (0.9 mm), weak, seemingly vestigial, lying at ventro-posterior end of cephalic hemocoel.

Etymology: From the Latin feminine noun meaning one who imitates, in reference to the deceptively close resemblance of the shell to that of *Hastula cinerea* (Born, 1778), with which it occurred in the type lot.

Table 1. Measurements (mm) of shell characters of *Terebra imitatrix* new species and *Hastula maryleeae* Burch.

Species	Character	$\bar{x}$	Range	SD
T. imitatrix	Shell length	27.3	24.1–29.7	1.9
	Shell width	6.4	5.7–7.4	0.5
	Protoconch width	0.50	0.46–0.52	0.03
H. maryleeae	Shell length	18.2	15.0–24.1	2.7
	Shell width	4.6	3.7–5.5	0.6
	Protoconch width	0.40	0.38–0.42	0.02
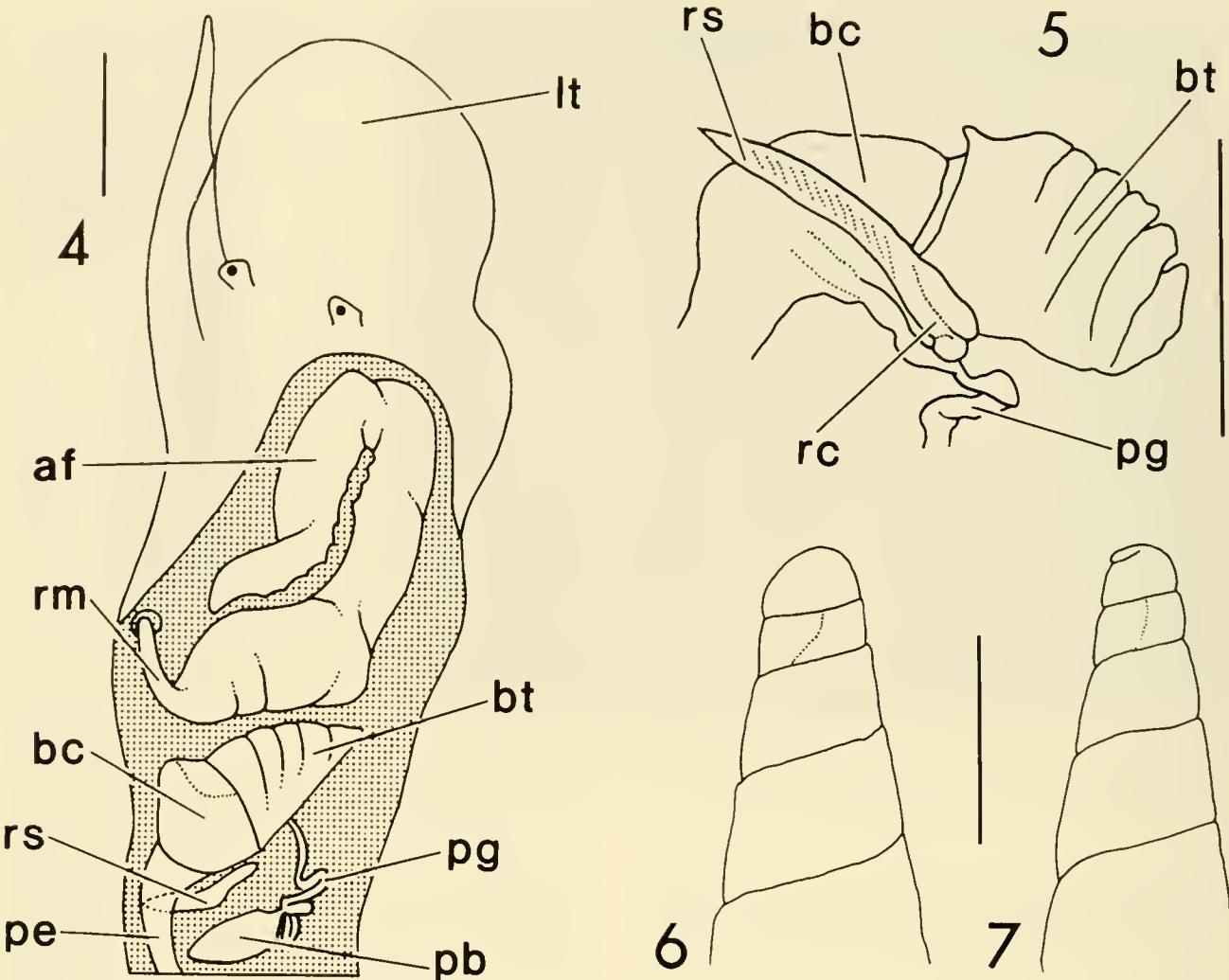
Figures 4–6. *Terebra imitatrix* new species. **4.** Diagrammatic dorsal view of the organs of the foregut. **5.** Right side of the buccal tube showing radular organs and insertion of the poison gland. **6.** Protoconch. **7.** *Hastula maryleeae* Burch, protoconch (AMNH 191815). Scale bars = 1 mm. af, accessory feeding apparatus; bc, buccal cavity; bt, buccal tube; lt, labial tube; pb, poison bulb; pe, pre-ganglionic esophagus; pg, poison gland; rc, radular caecum; rm, retractor muscle; rs, radular sac.

Type locality: Brazil, Rio Grande do Norte, sand island at mouth of the inlet at Areia Branca, 04°57′S, 37°08′W, G. & M. Kline et al., 14 December 1963.

Holotype: ANSP 299957, shell length 27.5 mm, width 6.7 mm.

Paratypes: Paratypes 1–20, ANSP 369293, from the type locality (15 dry, 5 in alcohol). Paratypes 21–22, UF 115180, from type locality. Paratypes 23–24, AMNH 129280, Brazil, Ceara, Acaraú, 02°53′S, 40°07′W.

Distribution: Presently known only from northern Brazil.

Ecology: Based on the locality label of the type lot, this species is found in sand near or at inlets much like some populations of *Hastula*. One specimen of *Hastula cinerea* (Born, 1778) was found in the type lot and another (AMNH 129269) from the same locality as the AMNH-

paratypes. Although these two species may occur microsympatrically, we assume there is no trophic competition due to the strikingly divergent feeding organs (see discussion).

Comparative remarks: *Terebra imitatrix* is similar in shell morphology to the West Atlantic *Hastula cinerea* group. It can be easily separated from *Hastula cinerea* and *Hastula salleana* by the lack of spiral rows of pits and the generally more numerous, but less prominent, axial ribs. Although similar in size, *T. imitatrix* is usually broader anteriorly. *Hastula cinerea* and *H. salleana* have 3.5–4.0 protoconch whorls, while *T. imitatrix* has 1.5–2.0. The typical color pattern of *T. imitatrix* is more distinctly banded with larger and more distinct brown spots at the suture and a broader white subsutural band. *Terebra imitatrix* and *Hastula maryleeae* are more difficult to separate, particularly southern Caribbean pop-

ulations of *H. maryleeae* described as *Terebra toba-goensis* Nowell-Usticke, 1969, now placed in the synonymy of *H. maryleeae* by Bratcher and Cernohorsky (1987). Examination of the lectotype (AMNH 195453 designated by Bratcher and Cernohorsky, 1987:194, pl. 60, fig. 235c) and paralectotypes (AMNH 191819) of *T. tobagoensis*, as well as several other lots from Tobago, typical specimens of *H. maryleeae* from Texas, and spec-imens of a weakly ribbed form of *H. maryleeae* from the Dominican Republic (see Bratcher and Cernohorsky, 1987, for discussion) revealed consistent shell characters by which the two species may be separated. Anatomical features are discussed below. Typical *H. maryleeae* is easily separated from *T. imitatrix* by the distinctive shell shape caused by the enlarged nodes of the axial ribs at the suture and by the slight crenulations at the sutures of the upper whorls. *Hastula maryleeae* has a much smaller shell than *T. imitatrix* at the same whorl count (table 1). The shell of *T. imitatrix* broadens more an-teriorly and has a proportionately slightly larger aper-ture. The protoconchs of both species have 1.5–2.0 whorls, however, the protoconch of *T. imitatrix* is more bulbous (figures 6, 7; table 1). Typical *T. imitatrix* also resembles the West African *Hastula aciculina* (Lamarck, 1822), particularly in color pattern. However, *T. imitatrix* lacks the supra-sutural groove and callosity found in *H. acic-ulina* (Bouchet, 1982; Bratcher and Cernohorsky, 1987).

DISCUSSION

Miller (1970) proposed a division of the Terebridae into three major groups based on the anatomy of the foregut (feeding type) and later published a series of papers (Miller, 1971, 1975, 1979) on this subject supported by in-depth life history studies. These data are reviewed and the species assigned to each group are listed in Bratcher and Cernohorsky (1987). Type 1 species have a long labial tube and a short buccal tube. They do not possess a radular apparatus or poison organs. This group is further divided into two subgroups, IA and IB, based primarily on habitat and prey (see Bratcher and Cer-nohorsky, 1987). Type II encompasses species exhibiting typical toxoglossan feeding characters. The labial tube is long and eversible and the buccal cavity is relatively large. The buccal tube is long and retractile. They have a poison gland and bulb as well as a radular sac containing two rows of harpoon-like radular teeth. This feeding type is further divided into two subgroups, types IIA and IIB, based primarily on habitat and behavior. Type IIA in-cludes several Indo-Pacific species, as well as the West Atlantic *Hastula* discussed in this paper (see Bratcher and Cernohorsky, 1987). Type III species possess an ac-cessory feeding organ which grasps prey and pulls it into the labial cavity. They lack a radular apparatus and some have lost the buccal tube and salivary glands. This group presently contains no Atlantic species, but is represented by several Indo-Pacific taxa (see Bratcher and Cerno-horsky, 1987).

Terebra imitatrix has very different foregut anatomy

Figures 8, 9. Radular teeth of paratype (ANSP 369293) of *Terebra imitatrix*, new species. **8.** Whole tooth, 60 ×. **9.** Tip of tooth, 200 ×.

from the West Atlantic *Hastula*. We have dissected *H. salleana* and *H. maryleeae* for comparison, and both possess a Type IIA polyembolic proboscis (Miller, 1970, 1971). *Terebra imitatrix* has a large spoon-shaped labial tube, presumably ineversible, a labial cavity dominated by the accessory feeding apparatus, an extremely short buccal tube incapable of extending outside the mouth and the buccal cavity, and the associated radular organs are minute in comparison to those of *Hastula*. The ves-tigial poison gland and bulb are barely recognizable as such and are considered homologous to the massive poi-son gland and bulb of *Hastula* only by the similarity of position and the site of its entrance into the buccal cavity. The radular teeth are similar in size and shape to those of *Hastula maryleeae* (0.15 mm). The teeth of *H. sal-leana* and *H. cinerea* are larger (0.5 mm) and barbed. The presence of an accessory feeding apparatus and the small size of other foregut organs place *T. imitatrix* near the group possessing a Type III polyembolic proboscis. However, the presence of radular and poison organs, such as occur in *T. imitatrix*, has not been reported for this proboscis type. Also, the shell of *T. imitatrix* is very different from the species in this group, all of which have shells with deeply impressed sutures, a sub-sutural groove and strong to moderate axial sculpture.

The feeding behavior of *Hastula cinerea* and of *H. inconstans* (Hinds, 1844) have been well documented by Marcus and Marcus (1960) and Miller (1979), re-spectively. The long eversible labial tube forages for prey items. A single radular tooth is passed through the labial tube, held in the tip, and inserted into the prey to fa-cilitate penetration of the venom. The prey is then in-gested via the labial tube. Miller (1970) suggests that species with a Type III proboscis forage by utilizing the accessory feeding apparatus, and that food items are passed into the opening of the interior buccal tube. We do not know if the radular and poison organs are func-tional in *Terebra imitatrix*. If so, the radular tooth is either transferred from the buccal tube to the accessory feeding apparatus and inserted into prey outside the body, or once it reaches the buccal tube.

The presence in *Terebra imitatrix* of the accessory feeding apparatus recorded in a few Indo-Pacific *Terebra* and the poison and radular organs of *Hastula* make this species unique. *Terebra imitatrix* may be closely related to the West African species, *Hastula aciculina*, however, this species must be studied anatomically before this assignment can be verified. Generic limits within the Terebridae are presently poorly understood with much overlap in shell and anatomical characters. Additional anatomical studies are needed to clarify the taxonomic and evolutionary significance of the foregut in the Terebridae.

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Notes on the Biology and Morphology of *Margaritifera hembeli* (Conrad, 1838) (Unionacea: Margaritiferidae)

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ABSTRACT

The freshwater pearl mussel *Margaritifera hembeli* is found only in the Red River basin and a few nearby drainages in Louisiana. Though of concern to conservationists because of its declining numbers, *M. hembeli* remains virtually unknown with respect to its anatomy and biology. The species contains all the anatomical characters that typify margaritiferid species. The sexes are separate and the gonads show a definite seasonality in activity. Gametogenesis is pronounced in specimens collected in the fall, followed by degeneration of reproductive tissues in the late winter through to late spring. It is concluded, on the basis of observed gonadal activity, that oviposition and spawning take place between late November and late January. Characters are evident in the morphology of the visceral nervous system and the stomach of *M. hembeli* that clearly distinguish *M. hembeli* from *M. marrianae* and other eastern North American margaritiferid species. A distinct relationship between *M. hembeli* and *M. marrianae*, however, is suggested by the mutual occurrence of lateral hinge teeth and a corrugated surface of the posterior portion of the shell. Due to the lack of knowledge of the anatomy and biology of other margaritiferid species, especially those living in Asia, it is premature to suggest relationships between *M. hembeli* and other described margaritiferid species, particularly those with lateral hinge teeth.

Key words: *Margaritifera*; anatomy, reproduction, North America.

INTRODUCTION

The North American freshwater mussel *Margaritifera hembeli* (Conrad, 1838) was once believed to comprise two geographically discontinuous populations taxonomically linked by vague similarities of the shell. Johnson (1983) separated the two populations taxonomically by describing the Alabama group as *M. marrianae*, thus restricting the *M. hembeli* group to Louisiana. His description included characters of the shell only, principally the degree of sculpturing on the shell surface and the shape of the ventral shell margin. Additional conchological differences between the Louisiana and Alabama populations were noted by Smith (1983) who pointed out dissimilarities in the mantle-shell attachment scars on the inner nacreous surface.

Margaritifera hembeli probably had a more extensive range in the Red River drainage as indicated by museum records, particularly a specimen in the American Museum of Natural History (AMNH 193786) from the Red River in Arkansas. During the present century, however, the range has contracted considerably due to deteriorating environmental conditions. The present range is limited to the Bayou Teche drainage (Vidrine, 1985) and a single stream in the Red River drainage. The drastic reduction in range has elicited concern from the federal government, which has provided protection for the remaining populations (Stewart, 1988).

Despite increased concern for *M. hembeli*, very little is known about this species other than the characteristics of its shell. Ortmann (1912) provided a brief description of the anatomy of *M.* "*hembeli*," but the specimens upon which he based his description came from Alabama and, therefore, are appropriately referred to *M. marrianae*. Hence the anatomy of *M. hembeli* remains undescribed, and nothing is known about its biology. The present study provides some information on gonadal activity and details of the anatomy of the stomach and nervous system. Comparisons are made with other North American margaritiferid species, including *M. marrianae*, as studied by Smith (1979a, 1980, 1986, and unpublished).

MATERIALS AND METHODS

A total of 43 partially or completely relaxed, preserved, specimens were studied. All were collected on various dates from 1973 to 1986 from Brown Creek, Gardner, Rapides Parish, Louisiana. Specimens had been fixed in 10% formalin, washed in water, and stored in 50% isopropyl alcohol. Five specimens lacked information on date of collection and were utilized for dissection purposes only. The remaining lots were used for histological investigations of gonadal activity and sexual characteristics, as well as for anatomical studies. The collection dates and numbers of specimens used in the study of gonadal activity were as follows: October 1, 1973 (1 specimen); October 5, 1974 (4 specimens); February 22, 1975 (8 specimens); March 28, 1975 (4 specimens); April 25, 1975 (3 specimens); June 21, 1975 (2 specimens); March 30, 1986 (5 of 16 specimens).
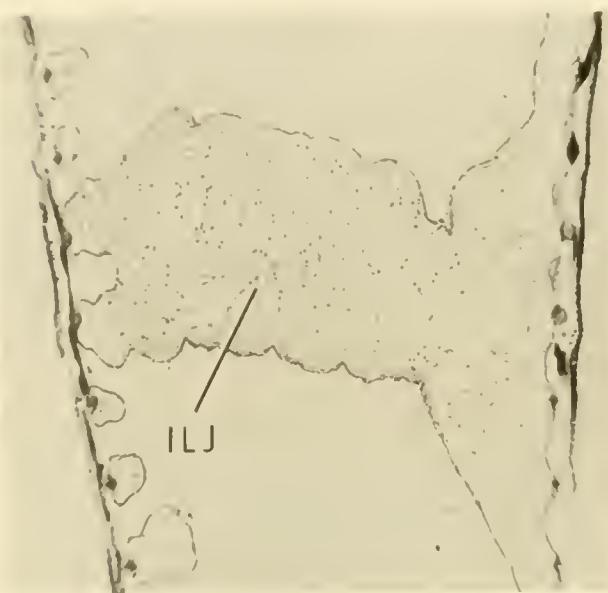
Figure 1. Photomicrograph of a transverse section through the gill of *Margaritifera hembeli* showing the interlamellar junction (ILJ), 30 ×.

Figure 2. Photomicrograph of a transverse section through the posterior portion of the mantle of *Margaritifera hembeli* showing the partially contracted diaphragmatic septum (DS), which separates the exhalent (EX) and inhalent (IN) chambers, 80 ×.

Portions of the viscera of each specimen were infiltrated with paraffin, sectioned at seven micrometer thickness, and stained with Ehrlich's hematoxylin and eosin. Some sections were stained in a picro-ponceau connective tissue stain following the method described in Humason (1979:147). At least five slides were prepared for each specimen. The barren gills of two specimens and a portion of the posterior mantle lobe of one specimen were also sectioned in a similar manner and stained with picro-ponceau connective tissue stain.

Dissections were undertaken on the stomach and visceral nervous system of eight specimens. Three specimens were investigated for gross morphology of the gills, nervous system, and excretory system. The method of dissection and exposition of specific internal organs, and the terminology used to describe various organ components, follows Smith (1980, 1986).

All material relevant to this study has been cataloged in the invertebrate collections of the Museum of Zoology (Nos. MO. 1643–1645), University of Massachusetts, Amherst, Massachusetts.

RESULTS

Gross Anatomy

Anterior and posterior adductor muscles subequal, foot musculature and associated pedal and retractor muscles well developed. Cerebral and pleural ganglia fused, kidney with both glandular and non-glandular chambers, renal pore and gonopore closely set but clearly separate. Labial palps falcate and large, gills or demibranchs lamellar, inner gill larger than outer gill, both inner and outer gills free from mantle posterior to pallial line. Both
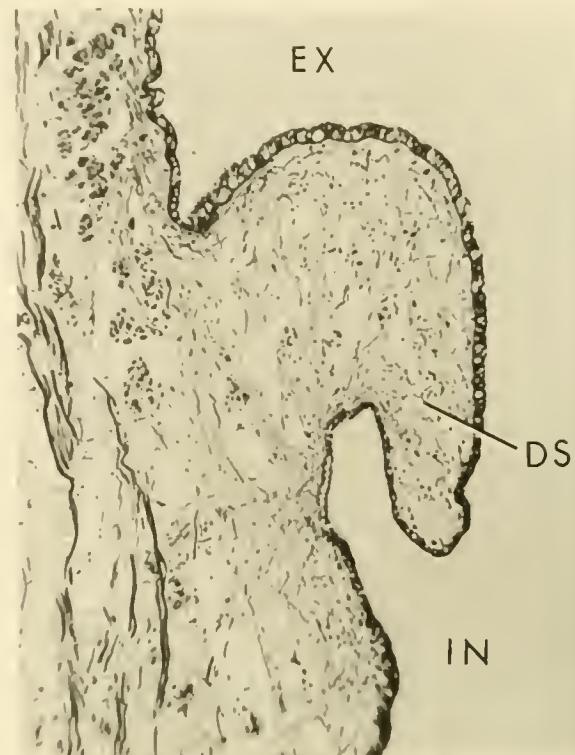
lamellae of each gill held together by solid, separate interlamellar junctions (figure 1, ILJ), lined with squamosal epithelium and composed of loose connective tissue and fine fibers that are more muscular appearing than collagenous (in *M. margaritifera*, see Smith, 1979a). Interlamellar junctions for the most part arranged in oblique rows in typical margaritiferine fashion (Ortmann, 1912; Smith and Wall, 1983: fig. 1b), similar to gills of *M. marrianae* (Ortmann, 1912:235). Gill junctions are somewhat patternless along lower margin and anterior and posterior extremities of each gill plate.

Mantle lobes free all around, no indication of division of exhalent region of mantle margins into separate anal and supra-anal apertures. Inhalent and exhalent chambers separated posteriorly by diaphragmatic septa (figure 2, DS), and though not observed in the living animal, are presumed to function similar to *M. margaritifera* (Smith, 1980). Inhalent margin of mantle with densely pigmented papillae, exhalent region pigmented, with cremulate margin.

Gonadal Activity and Sexuality

All animals examined histologically were sexually mature, including several small specimens ranging in shell length from 49 to 69 mm (believed to be from 6 to 9
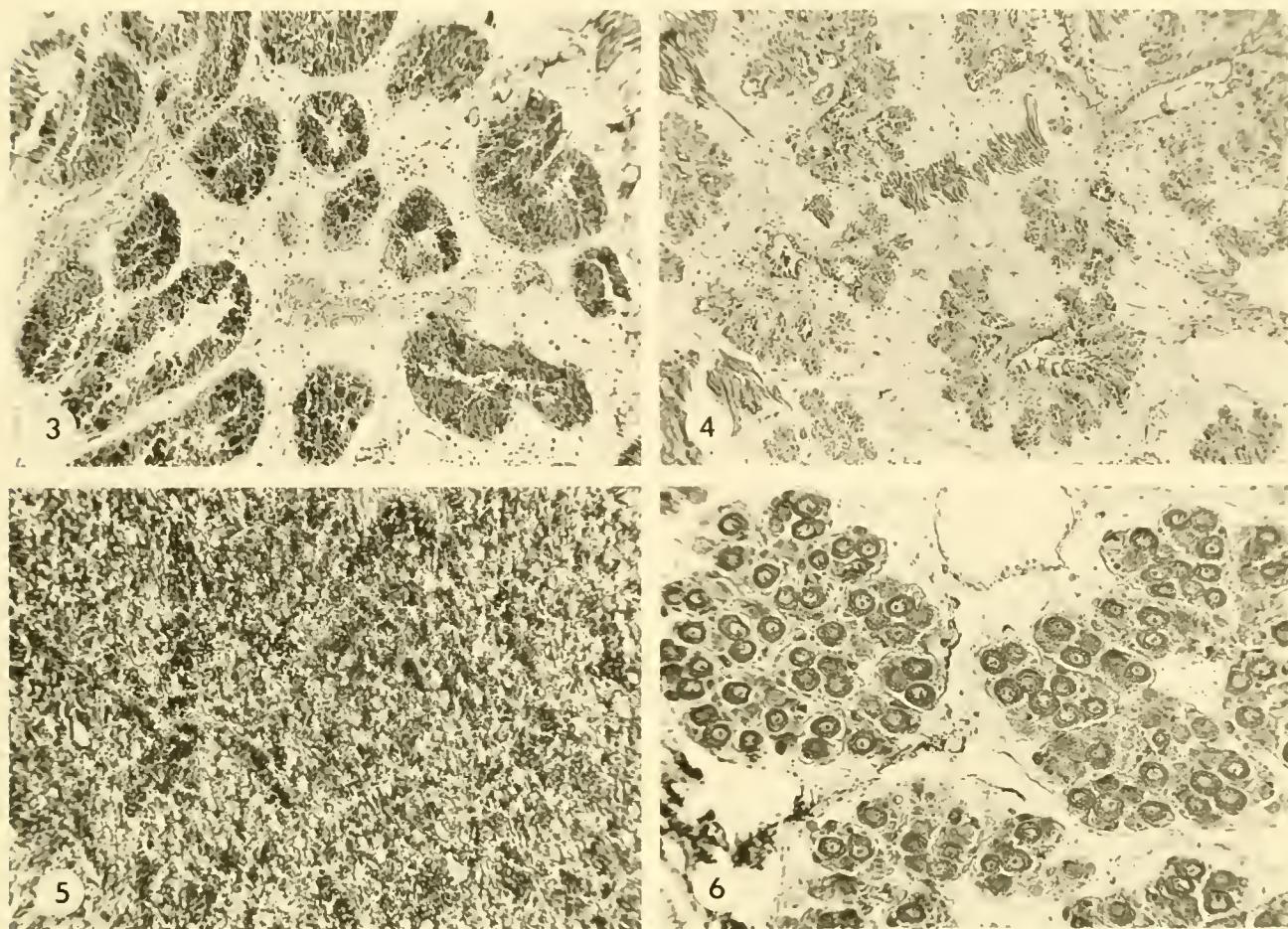
Figures 3–6. Photomicrographs of histological sections through male and female gonads of *Margaritifera hembeli*. **3.** Gonad of a male specimen of *M. hembeli* collected in February, following spawning of gametes, 65 ×. **4.** Gonad of a female specimen collected in February following spawning, 65 ×. **5.** Gonad of a male specimen of *M. hembeli* collected in October and showing male gametes which have filled the entire gonadal stroma, 100 ×. **6.** Gonad of a female specimen of *M. hembeli* collected in October and containing fully developed ova, 100 ×.

years old on the basis of shell annuli). This would suggest that *M. hembeli* matures at an earlier age than North American *M. margaritifera* (Smith, 1979b). No evidence of hermaphroditism was observed.

Although no gravid females were among the available specimens, a specific reproductive cycle was indicated by the gonads of sectioned specimens. Animals collected in February, March, and April showed characteristic post-spawning features (figures 3, 4) including partial or complete occlusion of gonadal acini by granules, presumed pycnotic cells, and unspawned gametes in various stages of development or cytolysis. Animals collected in June showed little change from April specimens indicating that complete resorption of reproductive tissues, corresponding to an undifferentiated stage of non-reproductive activity, apparently does not occur. By early October, gonadal activity is resumed and sex cells, including the latter stages of spermatogenesis and oogenesis, are abundant within all observed acini (figures 5, 6). It is therefore hypothesized that the oviposition of eggs into marsupial demibranchs and the spawning of male ga-

metes takes place sometime between late November and late December with release of larvae occurring in late December or January. Based on examined specimens, there is no evidence that production of glochidial larvae takes place at any other part of the year.

Visceral Nerve Anatomy

In *M. hembeli*, the first pallial bifurcation (figure 7, BI) of the posterior nerve is well anterior of the mantle nerve separation, usually arising from the visceral ganglion itself at a point near the origin of the posterior nerve cord (figure 7, PNC). Some variation exists in the position of this bifurcation relative to the visceral ganglion. The overall pattern differs from that observed in other eastern North American margaritiferids including *M. marrianae*, in which the first bifurcation is normally posterior of the visceral ganglion, but similar to that observed in *Cumberlandia monodonta* (Smith, 1980, unpublished data). Moreover, in both *M. hembeli* and *M. marrianae*, the accessory nerve, which is typically present in *M.*

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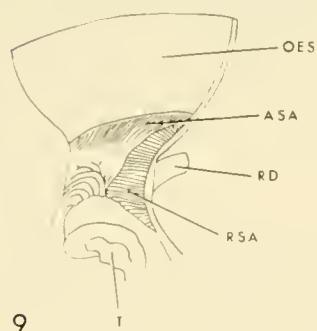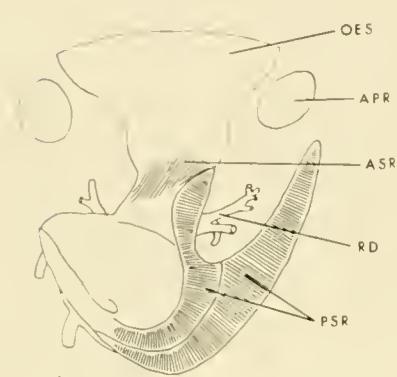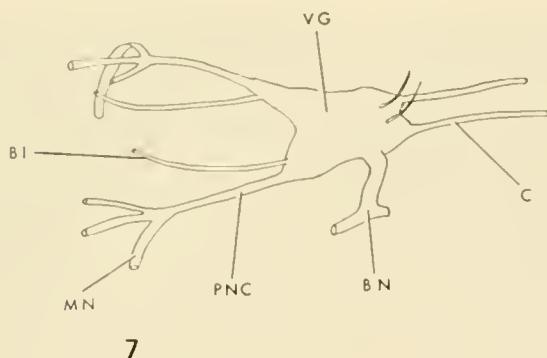
Figures 7–9. Anatomy of the visceral nervous system and stomach of *Margaritifera hembeli*. **7.** Visceral ganglion (VG) of *M. hembeli*, 20 ×. **8.** Morphology of the stomach roof of *M. hembeli*, 5 ×. **9.** Morphology of the stomach floor of *M. hembeli*, 5 ×. APR, anterior protractor muscle; ASA, anterior sorting area; ASR, anterior sorting area of roof; BI, first pallial bifurcation; BN, branchial nerve; C, commissure to cerebro-pleural ganglion; MN, mantle nerve; PNC, posterior nerve cord; OES, esophagus; PSR, posterior sorting area; RD, right duct; RSA, right side sorting area; T, major typhlosole.

margaritifera and *C. monodonta* (Smith, 1980), is almost always absent, being observed only once in *M. marrianae* (Smith, unpublished data).

STOMACH ANATOMY

In addition to the posterior sorting area, which is typical of other eastern North American margaritiferids, the stomach roof of *M. hembeli* contains a well developed anterior sorting area and a continuation of the posterior sorting area extending along the right side of the stomach roof and separated from the anterior sorting area by a ridge (figure 8).

The floor of the stomach interior (figure 9) is characterized by an anterior sorting area that is somewhat similar to *M. marrianae* (Smith, 1986: fig. 4b); however, the right side sorting area of *M. hembeli* is completely unlike *M. marrianae* in that a distinct platform is absent in *M. hembeli* and the sorting ridges run primarily laterally, rather than in the anterior-posterior pattern seen in *M. marrianae*. A groove sets off the right side sorting area from the anterior sorting area in *M. hembeli* and the morphology of the stomach floor sorting areas of *M. hembeli* can be considered more similar to *M. margaritifera* in overall appearance than to other eastern North American species.

DISCUSSION

As demonstrated by anatomical investigations of the visceral nervous system and the stomach (this study), and conchological differences discussed elsewhere (Johnson, 1983; Smith, 1983), *M. hembeli* and *M. marrianae* clearly represent distinct lineages within the genus *Margaritifera*. Although both species have lateral teeth, these teeth are also present in *M. auricularia* (southern Europe) and *M. laosensis* (southeast Asia). Lateral teeth may therefore represent structures that have arisen separately in different "stocks" of margaritiferid species, or may be symplesiomorphies indicative of an ancestral relationship.

The presence of a corrugated surface of the posterior slope of the shell (weakly expressed in *M. hembeli*) and the close geographical proximity of these two species are the strongest lines of evidence indicating a relationship between them. Nevertheless, the pattern of visceral nerve bifurcation and stomach morphology in *M. hembeli* and *M. marrianae* show interspecific variation as great as that observed between either of these two species and *M. margaritifera* or *C. monodonta*. Biochemical data of the sort developed for *M. margaritifera*, *C. monodonta*, and *M. hembeli* by Davis and Fuller (1981) is not available for *M. marrianae*, precluding a comparison of genetic distances among the four species. However, the available biochemical data (Davis and Fuller, 1981), combined with anatomical information presented in this study and elsewhere (Smith, 1980, 1986), clearly supports the concept that the North American species of the Margaritiferidae have been isolated from one another for a considerable period of time (Smith, 1976).

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The Two Printings of J. F. Gmelin's *Systema Naturae,* 13th Edition (1788–96)

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One of the more important 18th century reference works in systematics is J. F. Gmelin's 13th edition of Linnaeus' *Systema Naturae.* This work represented a considerable updating of and expansion upon the 12th edition of the *Systema Naturae* (Linnaeus, 1767). Gmelin not only provided additional bibliographic references for the species described by Linnaeus, but he also described numerous new species, using the same format as had Linnaeus. Gmelin's magnum opus was published in three volumes, comprising 10 parts altogether: *Regnum Animalium* (7 parts); *Regnum Vegetabile* (2 parts); and *Regnum Lapideum* (1 part). For comments on the structure and content of Gmelin's work, see Dodge (1958:157–158).

Few systematists, however, have realized that Gmelin's work actually underwent two separate printings. The initial German printing was by Georg. Emanuel. Beer of Lipsiae [= Leipzig]; the later French printing was by J. B. Delamollière (subsequently as Bernuset, Delamollière, Falque et Soc.) of Lugduni [= Lyon]. Both, of course, were written in Latin.

Hopkinson (1907) provided a valuable collation of the Lipsiae printing, based on an analysis of various German literature abstracts and review publications. He noted that only the first part in the two multi-part volumes had a date on the title page and that this date "did not apply to the whole of the parts in that volume" (Hopkinson, 1907:1036), since the later parts were published in following years. Hopkinson did not refer to the Lugduni printing. Agassiz (1852:69) listed this work as "Leipz. 1788–1793, . . . Lugduni, 1789–1796." Engelmann (1846: 103) provided the same dates as had Agassiz, but erroneously gave the place of publication as "Lugd. Batav." which is actually Leiden [= Lugduni Batavorum]. Sherborn (1902:xxxv) gave the same dates, made the same geographical transposition as had Engelmann, and specified that the second printing was a reprint of the first. Hulth (1907:13) and Soulsby (1933:16, 50) provided a partial collation of these two printings; however, their dates are based solely on those stated on the title page for the first part of each of the two multi-part volumes. Stafleu and Cowan (1976:956) briefly mentioned the two

printings, and noted for the Lugduni printing: "type reset, no copy seen". Frequently, library copies will have the same date stamped on the binding of each part or hand-written on the first page of each part; this is incorrect. The important facts are that the Lugduni printing was published *after* the Lipsiae printing, and was printed from reset type which resulted in a number of differences due to printer's error. Therefore, the date of publication of each part of the Lugduni printing must post-date that of the relevant part of the Lipsiae printing.

Unfortunately, we have not been able to determine the date of publication for the succeeding parts of the Lugduni printing (only for the first part in the multi-part volumes). However, we present this comparison here in order to alert systematists to the existence of these two printings. Should the reader know of further bibliographical sources bearing on this matter, we would greatly appreciate hearing from them.

Herein we present as complete a collation as possible of the two printings of Gmelin's *Systema Naturae,* based on Hopkinson (1907) and on our examination of complete sets of this work in the libraries of the Museum of Comparative Zoology, the British Museum (Natural History), and the Muséum National d'Histoire Naturelle, Paris.

Gmelin, Jo. Frid. [Johann Friedrich]. 1788–1793. Caroli a Linné, Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Editio Decima Tertia, Aucta, Reformata. Georg. Emanuel. Beer, Lipsiae; [Second printing, 1789–1796], J. B. Delamollière, Lugduni.

Tomus 1, REGNUM ANIMALIUM

I (1) Mammalia to Aves Picae, pp. xii + 1–500
      Lipsiae, 1788; Lugduni, 1789.
I (2) Aves Anseres—Aves Passeres, pp. 501–1032
      Lipsiae, 1789; Lugduni (post 1789?).
I (3) Amphibia—Pisces, pp. 1033–1516
      Lipsiae, 1789; Lugduni (post 1789?).

Tomus II, REGNUM VEGETABILE

Tomus III, REGNUM LAPIDEUM

It has been our experience that molluscan taxonomists who have used Gmelin's work have usually referred solely to the Lipsiae printing. Among others, these include Dodge (1958:157–158); and Kohn (1966) who provided biographical information on Gmelin and a useful critique of his work. An example of the taxonomic problems that can arise with respect to the two printings of Gmelin's work is that of certain species of Cancellariidae (Gastropoda) reviewed by Petit (1984). For *Buccinum piscatorium* Gmelin, 1791 (p. 3496), the Lipsiae printing gave two references: "List. Conch. t. 1024 f. 89" and "Martin. Conch. 4. t. 124 f. 1151, 1152". Based on this, Petit chose the figures from the latter reference (*i.e.*, Chemnitz, J. H., 1780, *Neues Systematisches Conchylien-Cabinet*, Vol. 4, Nurnberg) to be representative of this species. Subsequently, A. Verhecken (*in litt.*) inquired as to how the Chemnitz illustration could be used in this manner since it was not cited by Gmelin. In later correspondence, Verhecken advised that he had found that he was referring to a copy of the Lugduni printing. In that printing only one reference, the aforementioned "List. Conch. t. 1024 f. 89" (*i.e.*, Lister, M., 1692/1770, *Historiae sive Synopsis Methodicae Conchyliorum*, London), was given for the species in question; the Chemnitz reference being omitted. Obviously, the omission of the reference to Chemnitz was a printer's error, as a comparison of the two printings makes it evident that the type was reset and errors were made.

Incidentally, the third volume of this work (the *Regnum Lapideum*) was placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature (along with the related sections of Linnaeus and of Turton), since the "generic" names of fossil animals used in these works actually corresponded to the classes of Recent animals (ICZN, 1954, Opinion 296).

We conclude that (1) since the Lipsiae printing was published first, it should serve as the basis for discussion of Gmelin's species; (2) the Lugduni printing should be treated as a reprint (or reissue) in which errors occur, and not as a "second edition"; (3) systematists who are studying species described by Gmelin should compare the two printings in order to uncover any discrepancies with respect to species descriptions or references.

ACKNOWLEDGEMENTS

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